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Plumage Variability in Redpolls (*Carduelis flammea* and *C. hornemanni*, L.): A Test of Rohwer's Status Signalling Hypothesis

by

© Miriam L. Diamond

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Zoology

EDMONTON, ALBERTA

Fall 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Plumage Variability in Redpolls (*Carduelis flammea* and *C. hornemanni*, L.): A Test of Rohwer's Status Signalling Hypothesis submitted by Miriam L. Diamond in partial fulfilment of the requirements for the degree of Master of Science.

W. A. Fuller

Supervisor

Date 26 Aug/80

to my aunt,

Sarah Boroditsky Chernick

who guided, inspired, and taught me how to live

ABSTRACT

Rohwer's status signalling hypothesis postulates that intraspecific plumage variability has evolved to signal the approximate status of individuals in dominance hierarchies within species that flock during winter. His hypothesis was tested with redpolls (*Carduelis flammea* and *C. hornemanni*, L.), northern cardueline finches noted for extensive plumage variability. An extension of Rohwer's hypothesis, that brightly-coloured birds (those predicted to be dominant) should enjoy greater reproductive success than pale (subordinate) individuals, was also tested.

Data were collected from observations of breeding redpolls in Inuvik and Krekovick Landing, Northwest Territories, during the summers of 1977 and 1978. Contrary to the prediction based on Rohwer's hypothesis, the breast colouration of male and female redpolls was not correlated with nesting success, territory quality or frequency of mating. In order to test whether plumage colour can predict social status, experiments were conducted with captive redpolls during 1978 and 1979 in their summer and winter ranges. Unlike the observations reported by Rohwer (1977) for Harris' Sparrows (*Zonotrichia querula*) and Marler (1955b) for Chaffinches, (*Fringilla coelebs*), artificially coloured redpolls did not change status in hierarchies. Breast colouration of captive redpolls was not correlated with their agonistic behaviour, irrespective of season, morph (common or hoary) or level of aggression. Colouration

was described by the trichromatic coefficients dominant hue, purity and brightness and agonistic behaviour was described by the indices dominance, success, victimization and aggressiveness. Additionally, larger birds did not dominate smaller birds, again regardless of season, morph or level of aggression. Based on my observations and reports in the literature, I concluded that colour signals dominance status only insofar as colour and dominance are both sex- and age-related characteristics. An alternative hypothesis, that relative dominance in redpoll hierarchies is signalled by the behaviour of individuals rather than their colour, is presented. The colour variability exhibited by redpolls and other passerines may facilitate individual recognition. Aspects of the biology of redpolls and other passerines are presented in support of this suggestion.

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I: INTRODUCTION

The colouration of birds has long fascinated natural historians. More recently, ecologists have proposed theories relating social organization, community structure and physiology to the diversity of plumage patterns observed in birds. In 1975, Rohwer presented a new hypothesis that has sparked much attention. Rohwer postulated a link between avian plumage colouration and social structure, the status signalling hypothesis. He observed the following: colour variability occurs in species that associate in flocks during the winter and compete for resources through a dominance hierarchy in the flock; plumage monomorphism is found in species in which individuals are spaced over the environment and compete for resources through territoriality during the winter. Based on these observations Rohwer proposed that (a) Plumage variability has evolved to signal the approximate status of each individual in the social order and, (b) it is to the advantage of both dominant and subordinate individuals to signal their rank and assess others, thereby decreasing the necessity of fighting to determine relative status. This advantage should be greater in unstable flocks in which individuals are unknown to each other. (c) Lack of variability would be favoured in a territorial situation in which there are only two possible states--possessors and non-possessors of territories. Evolution of a single plumage signal would facilitate communication of possessorship state and recognition of

territorial competitors. Rohwer first investigated the general applicability of his hypothesis with a series of interspecific tests in which he examined plumage variability, social structure and habits of 29 passerine species (Rohwer 1975). He then used social interactions in a flock of wild Harris' Sparrows, (*Zonotrichia querula*), which exhibit wide variation in the extent of black colouration on the head and neck, for an intraspecific test of his hypothesis (Rohwer 1975). Rohwer found that brighter or "studlier" birds won 76 and 70 per cent of a random subset of 75 and 44 paired interactions respectively, results in agreement with his hypothesis.

The literature provides evidence that both supports and contradicts Rohwer's hypothesis. Marler (1955b) demonstrated that breast colour of captive Chaffinches (*Fringilla coelebs*), was correlated with the probability of winning intraspecific competitions. Female Chaffinches artificially coloured red to resemble males, won more encounters with males and females than normally coloured females. Red breasts caused an avoidance reaction in both sexes. However, his investigation was restricted to the role of sexual dichromatism, not the continuous variability that Rohwer addressed.

Observations inconsistent with Rohwer's hypothesis, that colour was unrelated to social status, were made by Brian (1949) in a study of wild Great Tits (*Parus major*), Thompson (1960) with captive House Finches (*Carpodacus*

mexicanus), and Dilger (1960) with captive Common Redpolls (*Carduelis flammea*). However, evidence presented to back their statements was scant. Bright colouration appears to be inversely related to social status in Purple Finches (*C. purpureus*), Cassin's Finches (*C. cassinii*; Samson 1977) and Bullfinches (*Pyrrhula pyrrhula*; Nicolai 1956; Hinde 1955, 1956), in all of which pale females dominate the brightly coloured males in winter flocks.

Balph, Balph and Romesburg (1979) specifically tested Rohwer's hypothesis with captive Dark-eyed Juncos (*Junco hyemalis*). The crown and throat colouration in this species varies with the sex and age of an individual. They observed six groups of six birds each, and concluded that hood colour was a poor indicator of social status between pairs of the same sex and approximately equal wing length, whereas sex was the better indicator of social status. They suggested that if plumage colouration signalled dominance status to flock members it was through learned association with other variables such as sex and age.

Baker and Fox (1978) also tested the relationship between dominance and social status with Dark-eyed Juncos. They reported a non-significant correlation between hood colour and rank, and that wing length predicted dominance best of those variables tested (sex was not tested). The conclusions they drew from observations of 21 captive birds were similar to those reached by Balph *et al.*: hood colour *per se* was weakly related to dominance, but it could predict

dominance by virtue of its association with sex.

Since the first presentation of his hypothesis Rohwer conducted further experiments which investigated control of cheating on the status signalling system in Harris' Sparrows. He found that sparrows artificially blackened to mimic high ranking birds were persecuted by those of high dominance status, and those bleached showed increased aggressiveness, attacking birds that treated them as subordinates (Rohwer 1977). Next Rohwer observed several birds in a flock of wild sparrows that were given testosterone and others that were given testosterone and dyed black. From these observations Rohwer concluded that the persecution he witnessed in the previous study was not due to a socially controlled signalling system as he first proposed, but rather was due to untreated birds perceiving an incongruence between the status signalled and the behaviour of the dyed birds.

A weakness shared by all the studies I have reported is their poorly quantified results. Assessment of colouration of individuals was achieved either implicitly or explicitly by subjectively comparing each individual to all others (Brian 1949, Thompson 1960, Dilger 1960, Balph *et al.* 1979, Baker and Fox 1978, Rohwer 1975, 1977, 1978) or colouration was treated as a discrete characteristic, for example, an individual either possessed male or female colouration (Marler 1955b).

In order to test the status signalling hypothesis

Rohwer (1975) and Balph *et al.* (1979) used the paired comparisons method in which only the direction of the outcome of an agonistic encounter is required. Baker and Fox (1978) tested Rohwer's hypothesis by correlating colour with dominance ranks. Both methods circumvent the need to quantitatively describe a bird's behaviour. Weaknesses of such methods are a lack of sensitivity to the magnitudes of outcomes and a simplistic view of dominance interactions, thus overlooking subtler behavioural details of interactions. Collias (1950) criticized a simplistic assessment of agonistic behaviour for its inability to provide an adequate measure of dominance and suggested using a multivariate measure as a better estimator. Finally, tests performed on rank data, such as the chi-square test of independence, are less powerful than tests that can be applied to continuous variables, such as regression or analysis of variance.

Another weakness of previous studies was small sample sizes. Dilger's (1960) comments on the relationship of colour and social status were based on eight birds intensively studied for an unspecified period of time. Although Rohwer (1975) and Balph *et al.* (1979) presented data for over 35 birds, the conclusions drawn by Rohwer and Rohwer (1978) were based on three experimentally treated birds and two controls. With so few animals sufficient replications of experimental treatments are indeed difficult.

Balph *et al.* (1979) have suggested that plumage variability has evolved in relation to breeding rather than winter social structure. In species that undergo a partial prenuptial (prealternate) molt such as Harris' Sparrows, this consideration is less important because summer plumage colouration is acquired independently of winter plumage. However, it is a relevant concern in juncos, carduline finches and several other passerines that molt only once a year and acquire their nuptial (alternate) plumage as a result of wear of the plumage obtained after breeding by the annual postnuptial (prebasic) molt (Dwight 1900). Examination of social behaviour with respect to plumage colouration in these species is necessary during both winter and summer.

Although it is generally assumed that body size is a predictor of dominance (e.g. Collias 1943, Thompson 1960, Fretwell 1969), evidence in the literature suggests that these two characteristics are poorly correlated in species that do not show exaggerated size differences (e.g. Shoemaker 1939, Tordoff 1954, Thompson 1960, Fretwell 1969, Rohwer 1975, Glase 1973). In these and other studies, body size has been estimated by a single variable--weight (e.g. Shoemaker 1939, Collias 1943, Thompson 1960), or wing length (e.g. Fretwell 1969, Rohwer 1975, Balph *et al.* 1979). However, the reliability of either variable in estimating overall body size has not been demonstrated.

It was the aim of this study to test Rohwer's

hypothesis of status signalling, specifically his prediction that an individual's colour serves to signal its dominance status in winter hierarchies of a variably-coloured species. In order to test this hypothesis, I developed methods to quantify agonistic behaviour, colouration and body size, and applied them to a large enough sample so that the results could be analyzed statistically.

The redpoll (*Carduelis flammea* and *C. hornemanni* L.), a northern cardueline finch noted for extensive plumage variability, was an ideal animal with which to test Rohwer's hypothesis. No explanations have been offered to account for the variability in plumage colouration exhibited by redpolls and other similar carduelines (specifically, variability within sex and age classes). The numerous hypotheses that have been proposed to account for avian colouration may be categorized according to the extent of variability they predict. For example, species of low colour variability would generally be expected if their colouration were used for camouflage, mimicry, physiological purposes, species recognition or flash colouration. Plumage patterns characteristic of each sex would result from sexual selection, use of colour signals for intrasexual threat or sex recognition. This categorization may over-simplify the predicted colour patterns, but nevertheless, none of the hypotheses listed predicts colour variability both within and between sex or age classes. The only hypotheses that address such colour variability are those of status

signalling (Rohwer 1975) and individual recognition (Bennett 1939, Hogan-Warburg 1966, Baylis 1979, Shields 1977).

The contention that the red areas of the redpoll are optical signals used in intraspecific communication is strengthened by the position and hue of the patches. The coloured crown, cheeks and breast are located frontally and ventrally where a conspecific, rather than, say, a predator, will view the colour (Rohwer 1975, Balph *et al*. 1979). Donner (1951, 1953), Goldsmith and Goldsmith (1979), Hamilton and Coleman (1933) and others have demonstrated that birds have excellent visual acuity and colour perception (comparable to that of humans). The rump patch may function in communication associated with flocking since it is more exposed when a bird is in flight than when its wings are folded. Red hues, common in many northern birds, should be favoured as signal colours where low sun-angles predominate for three reasons: (a) a bright signal such as red or orange would be most conspicuous where total irradiance is low, (b) these colours will appear brightest because they reflect most strongly in the portion of the spectrum with the highest ambient light levels (i.e. long wavelengths), and (c) those signals reflecting long wavelengths will be highly contrasted against blue sky or green foliage (Hailman 1977).

Therefore, because the majority of theories developed to explain avian colouration can be dismissed as unlikely with regard to redpolls, and because their colouration does

not appear to be a neutral characteristic attributable to such causes as dietary differences for example, redpolls appeared to be a highly suitable species on which to test Rohwer's hypothesis. Redpolls fulfill two important conditions Rohwer predicted would favour signalling in a species. First, redpolls are a variably coloured species that associate in winter flocks and compete for resources through a dominance hierarchy. Secondly, their flocks are of relatively unstable membership, therefore it would be advantageous for individuals to advertise and to be able to assess dominance status of unknown individuals, thereby reducing the need for combat to determine relative status.

Choice of redpolls for this study offered a further advantage. They could be observed during winter and breeding seasons which was necessary in order to test an extension of Rohwer's status signalling hypthesis to the breeding season; that brightly-coloured birds (predicted to be dominant) enjoyed greater reproductive success than pale birds (predicted to be subordinate).

II. STUDY ANIMAL

Redpolls are well known for their colour variability (Grinnell 1947, Newton 1972). Most birds possess a deep red poll or crown after their postjuvenal (first prebasic) molt, but the extent and intensity of red colouration on breast, cheeks and rump vary considerably from individual to individual. Males and adults of both sexes are generally redder than females and subadults, and Common Redpolls (*Carduelis flammea*) a darker red than the pink Hoary Redpolls (*C. hornemanni*). There is extensive overlap of plumage types within and between sex and age categories; consequently most individuals cannot be classified by colouration alone (Da Prato and Da Prato 1978, Evans 1966, Svensson 1975).

Redpolls are circumpolar in distribution. During summer they are found in northern boreal forest and tundra regions; during winter they come south to the boreal forest, northern deciduous forest, and prairies. They are largely nomadic, showing neither winter nor summer philopatry (Evans 1969, Eriksson 1970, Newton 1972, Davis 1977).

The social structure of redpolls is consistent with Rowher's observation that variably-coloured species associate in flocks. Redpolls feed in flocks year-round (Newton 1972). Flocks as large as 1,000 (Bowles 1917) and 4,000 birds (Easterla 1978) have been reported during winter. In summer, smaller aggregations of two to six birds are common. Based on the general hypotheses of Lack (1968)

and Crook (1965), Newton (1972) related the gregarious nature of redpolls to their graminivorous (seed) diet which is largely comprised of birch seeds which are patchily distributed (Peiponen 1962). Redpolls feed predominantly on seeds during summer (Grinnell 1947, Rising and Schefter, pers. comm.) unlike most winter graminivores which shift to insectivory (also from gregariousness to territoriality) while nesting.

Rohwer predicted that the advantage of status signalling should increase with flock instability. No direct evidence exists on the stability of redpoll flock membership. Shaub (1950) reported that 20 redpolls out of a total of 39 banded during a winter remained for nearly two weeks, but only three of the banded birds were observed in the area after three weeks. Eriksson (1970) concluded, from very low band returns during a winter and the following summer, that mortality amongst these birds was high. It seems likely however, that at least some of the 80 per cent disappearance reported for the three months November to January, was attributable to movement rather than death. My observations of banded redpolls at a winter feeder support the view that flocks are unstable in both location and membership.

Redpolls mate while in large winter flocks en route to breeding areas (Newton 1972). On the breeding grounds the monogamous pairs establish nests in semicolonial situations (Hilden 1969, Newton 1972). A clutch of four or five eggs is

incubated for 11 days by the female. The male feeds the female and any hatchlings from the time of nest initiation until the young fledge, from 11 to 13 days after hatching. Some studies suggest that two broods are reared within one season (Brandt 1943, Dice 1918, Grinnell 1947, Irving 1960, Hildén 1969, Troy and Shields 1979).

Little is known about predation on redpolls, a factor hypothesized to influence avian colouration (e.g. Cott 1946, Hailman 1977, Baker and Parker 1979). Kestrels (*Falco sparverius*; Cooke 1885), Marsh Hawks (*Circus cyaneus*; Roberts 1932), jaegers (*Stercorarius* sp.; Sutton 1932), Peregrine Falcons (*Falco peregrinus*; Sutton 1932), and Shrikes (*Lanius excubitor*; pers. obs.) have been observed to either capture or pursue wild redpolls.

The plumage colouration of redpolls is acquired in two ways. All birds one year old and older undergo a complete postnuptial (prebasic) molt whereas the first winter plumage of juveniles is the result of a partial postjuvenal (first prebasic) molt of body and wing coverts (Dwight 1900). Between annual molts feathers are abraded and change colour as a result: the white to gray barbules of the contour feathers break off and expose the carotenoid pigments that are restricted to the basal part of the feather (Dwight 1900). Thus, nuptial (alternate) plumage, which is redder than winter plumage, is acquired by wear rather than molting.

Carotenoid composition and concentration within the

feathers of birds can be determined by genetic, dietary, metabolic and physiological factors (Brush and Power 1976). From experiments performed on the House Finch, a close relative of redpolls, Brush and Power (1976) concluded that given a sufficient dietary source of carotenoids, colour variability, exhibited primarily among males, was due to hormonal activity and capacity to metabolize carotenoids. Deposition of pigments was ultimately expressed through follicular cell selectivity. Brush and Power suggested that dietary differences of wild House Finches contributed to their colouration differences. It is unknown how important this factor is in determining the colouration of wild redpolls. Although redpolls usually forage in flocks in which all individuals appear to consume the same foods, Troy and Springer observed pairs of nesting redpolls to travel different distances to feed and birds often varied considerably in the contents of their diverticula (Troy, pers. comm.). Nevertheless, it is unlikely that individuals choose seeds on the basis of carotene content (Brush, pers. comm.).

The effect of age on colouration is still uncertain. Michener and Michener (1931) concluded on the basis of returns of banded House Finches, that they increased in redness with age (however, old females never attained the bright colour of males). Kennard (1959, 1962) observed similar changesin Purple Finches. Band returns are extremely low in redpolls. Because they are nomadic, it has not been

possible to follow particular individuals. From very few returns it appears that redpolls may increase in redness with age (Troy, pers. comm.); however, as age was unknown when the birds were banded, colour changes may have been attributable to these birds passing from juvenile to adult stages. Increase of carotenoid deposition with age has not been demonstrated nor is there any physiological reason to believe it may do so, except that hormone levels could increase with age and affect colouration (Brush, pers. comm.).

Few data exist on the effect of hormones in determining colour variability. Tewary and Farner (1973) observed castrated male House Finches and those given estrogen, to grow female-like plumage lacking orange or red colouration typical of males. Similarly, Brush and Power (pers. comm.) found that House Finch males given antiandrogen, and females given testosterone, molted into female-like plumage (lacking red colouration). Males administered testosterone and dihydrotestosterone molted into normal male colour but variability was maintained within this group. These results demonstrate that sex hormones do in part determine plumage colouration, but that other, as yet unknown, factors contribute significantly to carotenoid metabolism and deposition.

The taxonomy of redpolls is controversial. Although Hoary Redpolls possess shorter, wider bills and generally lighter and less streaked plumage colouration than Common

Redpolls, birds of intermediate characters do exist and interbreeding occurs (Baldwin 1955, Kessel and Cade 1958, Maher 1959, Gabrielson and Lincoln 1959, Williamson *et al.* 1966). Several authors have concluded that two species exist despite extensive overlap of breeding populations and evidence of hybridization (Grinnell 1947, Wynne-Edwards 1952, Gabrielson and Lincoln 1959, Baldwin 1961, Osieck 1976). The American Ornithologists' Union (1957) lists *hornemanni* and *flammea* as distinct species (the generic name has changed from *Acanthis* to *Carduelis*; American Ornithologists Union 1976). Other authors have viewed Hoary and Common redpolls as a single species (Salomonsen 1928, Williamson 1961, Harris *et al.* 1965, Williamson *et al.* 1966). For example, Brooks (1968) suggested that common and hoary-types occupy endpoints of a physiological continuum with hoaries better adapted to cold than commons. Preliminary results of karyotyping Alaskan redpolls indicated no major chromosomal differences between the two types (Troy, pers. comm.). I accept the latter view of the taxonomic status of redpolls and thus regard commons, hoaries and hybrid types as one species.

III. STUDY AREA

Summer research was conducted at Inuvik (1977 and 1978) and Krekovick Landing (1978), Northwest Territories (Figure 1). Both are well within the geographic range in which redpolls are found. Inuvik (68° 18'N and 133° 29'W) is situated on the east shore of East Channel of the Mackenzie River Delta, at the edge of the open boreal biome (Aldrich 1967). Studies on captive redpolls were performed at an aviary at the Inuvik Research Laboratory (Department of Indian and Northern Affairs). Duck Lake, Hidden Lake and Bompas Street study areas were chosen after assessing redpoll activity in and immediately around Inuvik. The vegetation in which nests were situated at these sites differed somewhat from each other.

Duck Lake site, a 3 to 4 hectare woodland situated between the laboratory and east channel, supported the richest avifaunal community and redpoll population in the Inuvik area and so was the main area in which nesting activities were studied in 1977. It was dominated by spruce (*Picea glauca* and *P. mariana*) with a few birch (*Betula papyrifera*) on higher ground. Maximum height of trees was about 12 m. The other major vegetation, willow (*Salix* spp.) and birch (*Betula glandulosa*) shrubs attained heights of 5 m and densities of up to 40 stems/m^2. In places the shrub layer formed a thick canopy. Ground cover varied inversely according to canopy cover.

Figure 1. Locations of study areas.

Vegetation at the Hidden Lake site (just east of Inuvik) was similar to that at the Duck Lake site. At the Bompas Street site, the trees and shrubs were sparse and dwarfed compared with the Duck Lake site. The open spruce forest of this site was similar to the spruce woods described by Kessel and Schaller (1960) and Williamson and Peyton (1962) in their avifaunal studies of Alaska, and also resembled that found at Churchill, Manitoba (59° N, 94° W)(Ritchie 1959), the location at which Grinnell (1947) studied redpoll nesting.

In summer 1978, few redpolls nested in Inuvik, consequently another site, Krekovick Landing (69° 50'N, 128° 58'W) was chosen for most observations of redpoll nesting. The landing is located in a large tundra plateau on the eastern shore of the Anderson River Delta, 27 km from the Arctic Ocean.

Numerous plant communities were found within 5 km of the landing. Most redpoll activity occurred in the tall shrub community. In Alaska, Maher (1959), Williamson and Peyton (1962) and Williamson *et al.* (1966) and others reported that redpolls used a similar riparian community more heavily than other habitats. The tall shrub community may be divided into three subtypes: an *Alnus crispa* association in deep draws, a *Salix lanata* association in flatter and very wet stream beds and a *Salix alaxensis* association in less wet, open draws. *Salix* and *Alnus* shrubs in the *A. crispa* association attained heights of 2.5 to 3.5

m, below which a wide variety of herbs grew. The canopy height of the *S. lanata* association was 1 to 1.5 m. Only grasses, sedges and horsetails (*Equisetum* spp.) grew in the herb layer. The *S. alaxensis* canopy was 1.5 to 2 m in height and was less dense than that of the other two associations. Ground species were similar to those of the *S. lanata* association.

Medium shrub-heath community (Corns 1974, also named dwarf shrub sedge tundra by Maher 1959) was also used by redpolls around Krekovick Landing. Clumps of *S. glauca* from 0.3 to 3 m wide characterized this community which covered the central portion of the plateau. The height of the *Salix* shrubs varied from 0.3 to 1.3 m. Dwar birch, *Betula nana*, was much rarer than *Salix* and attained heights of only 0.3 m. Well-drained soils supported many herbs which were similar to those of the dwarf shrub community described by Kessel and Cade (1958), and Kessel and Schaller (1960), and the low shrub-heath community described by Williamson and Peyton (1962) and Corns (1974). However, those communities differed from the medium shrub-heath community in that the former were dominated by *Betula nana* rather than *Salix glauca*.

Nesting redpolls were also discovered on Bluff Island, that has an area of about 4 hectares and lies approximately 10 km south of Krekovick Landing in the Anderson River Delta. On the south of the wind-swept, sandy island grew sparse willow shrubs; the north part was covered by sedges.

Inuvik is in the taiga zone (Burns 1973), which is well within the climatic range of redpolls. Mean monthly temperatures during summer are cool (-0.8, 9.8, 13.3 and 10°C for May to August respectively, averaged over 14 years; Environment Canada, Temperatures and Precipitation 1941-1970, Y.T. and N.W.T.). Krekovick Landing, in the marine tundra zone (Burns 1973), is at the cold end of the climatic range in which redpolls breed. Mean monthly temperatures are about 5 C° cooler than at Inuvik (temperatures recorded at the closest weather station, Nicholson Point, 17 km north of Krekovick Landing). Mean total precipitation, mostly in rain, is low at Inuvik, particularly in early summer (17.5, 12.9, 34.3 and 46.2 mm total rainfall plus water equivalent of total snowfall for May through August respectively; Environment Canada, Temperatures and Precipitation 1941-1970 , Y.T. and N.W.T.). Krekovick Landing receives about 10 mm less precipitation than Inuvik during summer. Snow regularly falls at Inuvik and Krekovick Landing in all months except July. The sun remains above the horizon at both locations from late May to mid-July.

Winter research took place approximately 15 km southwest of Edmonton, in Parkland County, Alberta (Figure 1), an area typical of aspen parkland (Aldrich 1967) in which redpolls commonly winter. A shallow, tree-lined river valley runs east to west by the north border of the area. On either side of this valley lie strips of pasture that in

turn are bordered by cultivated fields to the north and south.

The climate of Edmonton is cold and temperate (Environment Canada, Temperature and Precipitation 1941-1970, Prairie Provinces). During winter mean monthly temperatures remain well below 0°C (-12.3, -16.3, -12.1, -7.3 and 2.9°C for December through April respectively). Mean total precipitation, mostly in snow, is low and relatively constant (18.5, 23.4, 19.8, 17.3 and 22.1 mm water equivalent, for December to April).

IV. METHODS

A. Capturing and Marking Birds

All birds handled in this study were caught in mist nets made of black nylon, of 3.2 and 3.8 cm mesh size, 2.1 m high, and 9.1 m, 12.8 or 18.3 m in length. The nets were placed in flight paths frequented by redpolls, i.e. along paths in the Duck Lake site and at the mouth of draws at Krekovick Landing. At the Winterburn site a platform 45 by 60 cm supplied with commercial finch seed mixture, was erected approximately 2 m in front of the aviary, and nets were placed to intercept redpolls flying from the platform to the birch and Manitoba maple trees 4 m away.

In order to capture parent birds at the nest in summer, a mist net was draped around the tree or bush in which the nest was situated, with an opening left to allow parents access to the nest. When either parent reached the nest it was frightened into the net.

At Kreckovick Landing some nests were in shrubs too short to support a mist net. In such circumstances two mist nests (either 9.1 or 12.8 m long) were erected in a V-shape to enclose the nest on 3 sides. The parents either inadvertently flew, or I scared them, into the net when they returned or left their nest.

Nets were set during the day but not during windy and/or wet weather conditions. In summer nets were checked hourly; in winter they were watched constantly. After the

birds were taken from the nets I put a standard U.S. Fish and Wildlife aluminum band stamped with a unique number, and two colour bands on the legs (tarsometatarsi) of each bird. All birds were identifiable by their unique band sequence at distances up to approximately 30 m.

B. Measurements

Size Measurements

For all birds captured the following measurements were taken as estimators of body size. Immediately after capture each bird was placed in a preweighed cotton bag, and the weight of the bird was taken to the nearest 0.1 g, with a Pesola scale that measured up to 30 gm. A set of six measurements including those traditionally used in ornithological studies (e.g. Barlow 1973, Emlen *et al*. 1975, Ricklefs 1977) were recorded to estimate bill and external body size (including feather length). Bill length, from the tip of the upper mandible to the anterior edge of the right nostril; bill width on the upper mandible, just anterior to the commissural point; and depth of the upper mandible taken perpendicular to the upper mandibular tomium at the base of the bill, were measured to 0.01 mm with a Mitutoyo dial caliper. Wing (chord) from the bend of the wing to the longest primary; tail length from the tip of the longest retrix to the uropygeal gland; and tarsus length from the proximal end of the tarsometatarsus to the last undivided scute were recorded to the nearest mm with the calipers.

Nineteen measurements (Figure 2, Appendix 2) were taken on the skeletons of those birds killed and autopsied. These measurements had the greatest coefficients of variation of a larger set first taken on redpoll skeletons (Troy, pers. comm.). Dial calipers were again used and the dimensions were measured to the nearest 0.01 mm.

Colour Determination

The colouration of all birds was estimated subjectively immediately after their capture. Under natural light in the summer, or incandescent and natural light in the winter, the intensity of red colouration on the cap or poll, cheek breast and rump of an individual were each scored on a scale of 0 (no red) to 5 (bright red). The colouration of birds handled in this study all fell within the white-pink-red colour range (except for a few yellow and orange caps): birds with salmon or orange-coloured breasts as Grinnell (1947) observed, were not encountered. The extent of red colouration on the breast was closely correlated with the subjective colour score I assigned a bird. Individuals that were assigned low scores had few, pale red feathers whereas individuals with high scores possessed a deep red colour over large areas of their breasts.

For birds captured and killed, colouration was measured after they were prepared as study skins, with a reflectance spectrophotometer, in order to provide a more objective description of the birds' breast colour than that assessed by eye (Bowers 1956). Feather colour did not change

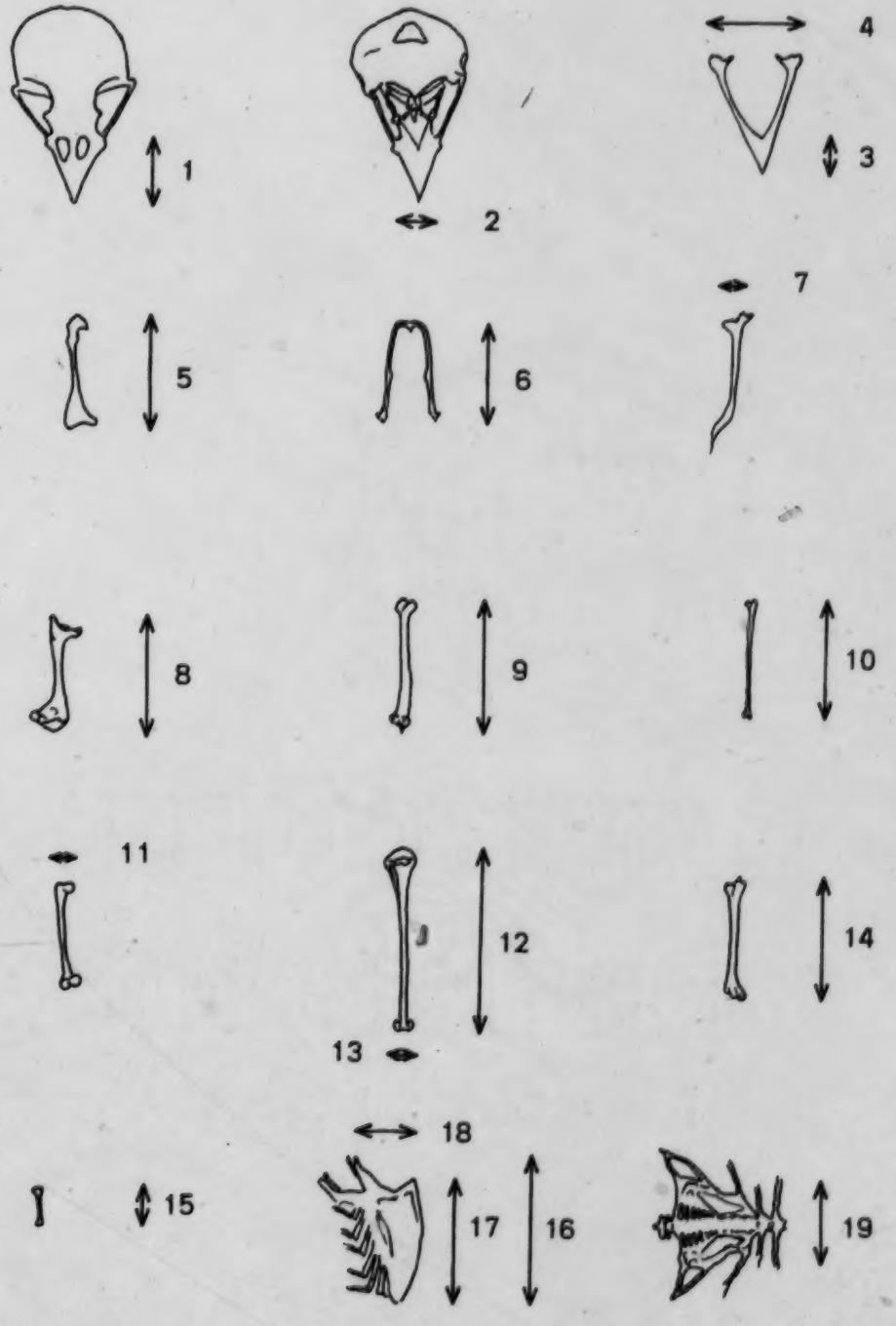

Figure 2. Illustration of skeletal measurements taken on redpoll specimens. Numbers refer to measurements that are described in Appendix 2. Bones are drawn to scale.

noticeably between the time of capture and colour determination. Measurements were made according to standard methods (established by the Commission Internationale de l'Eclairage or C.I.E.) with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance sphere located at the Royal Ontario Museum, in Toronto, Ontario.

Briefly, the spectrophotometer consists of a light source, a series of collimating lenses and prisms, the test sample, photoelectric detector and a recording device (Hardy 1936). The photoelectric detector compares the reflectance of the sample at each wave length between 400 and 700 nm, with the reflectance of a barium sulphate standard. Since rough textured or non-homogeneous materials scatter light from a collimating beam, an integrating or reflectance sphere is used. The white walls of the sphere reflect and re-reflect the incoming light and thus illuminate the sample from all directions (Dyck 1966). Use of the reflectance sphere allowed me to estimate colour as seen in the intact feather, which results from pigments and feather structure, rather than measure colour from the isolated pigments alone.

Tristimulus values were calculated by the weighted ordinate method (Hardy 1936) from the reflectance curve recorded after each spectral scan. These values (defined by the C.I.E.) are monochromatic primary red, green and blue or X, Y, and Z respectively. Y has been chosen by the C.I.E. to be both green and a measure of the luminous intensity of the

sample, the latter described as the total reflectance of all light relative to the standard (Bowers 1956, Dyck 1966). Subjectively, Y gives a measure of the brightness of a sample (Hardy 1936).

Since the tristimulus values can be difficult to interpret and compare (Hardy 1936), colours are usually described by means of the trichromatic coefficients. The coefficients, which are ratios derived from the tristimulus values, provide a unique numerical description of the quality of any colour, or its chromaticity. The first ratio, $x=X/(X+Y+Z)$, represents dominant wavelength or hue. Every real colour is a mixture of white light and spectrum light of the dominant wavelength. The second ratio, $y=Y/(X+Y+Z)$, is a measure of purity or saturation, which corresponds to the proportion of white light or the degree to which the colour differs from gray (Hardy 1936, Bower 1956, Dyck 1966 and Hailman 1977).

Breasts of redpoll specimens prepared as study skins, were positioned in front of the 11 mm spectrophotometer aperature and a 4 by 6 mm spot, that was approximately 2.5 to 5 percent of the red area of a breast, was illuminated (see Barlow and Williams 1971, for an explanation). The reddest, or if there was no red on the breast, whitest, area of the anterior of the breast (usually midway between the centre of the breast and beginning of the wing) was chosen for measurement. Because of the non-uniformity of the feather surface, two readings were taken from each bird from

this region and the reddest or whitest curve was chosen. The rationale for choosing the reddest or whitest curve from a bird was based on the assumption that a conspecific viewer would first perceive the most brilliant colour on the breast rather than an average of breast colour. In the absence of any red feathers on the breast, I assumed that the whitest part of the breast would first attract the eye given the high visual acuity and excellent colour perception abilities of passerines (e.g. Hamilton and Coleman 1933, Goldsmith and Goldsmith 1979, Donner 1951, 1953). The dominant hue value measured for each bird with the spectrophotometer generally agreed with the bird's assigned colour-score. (Spearman Rank Correlation, $r=0.69$).

C. Breeding

Nesting

My primary goal during the breeding season was to test the extension of Rohwer's status signalling hypothesis, that brightly or red-breasted birds were fitter than pale or white-breasted birds. The most direct way of testing this prediction was to compare nesting success of birds varying in colour; thus finding nests received priority during the breeding season. Redpolls usually build well-concealed nests. This, in addition to their lack of territorial site defense and the often shy, unobtrusive nature of the birds, made the task of nest finding difficult, a problem described by Grinnell (1947) and Clement (1968). Approximately 10 km^2

were searched for redpoll nests in Inuvik in 1977, 6 km² at Inuvik in 1978, and 10 km² at Krekovick Landing in 1978. Each nest discovered was marked by fluorescent surveyor's tape tied to a nearby tree or shrub no less than two meters from the nest.

In order to observe and identify birds attending 16 nests, parents were caught with mist nets, and banded and then released. At seven nests parents and young were captured when possible and killed so that their colour could be measured with the spectrophotometer.

Nests were visited every third day in 1977, and every fourth day in 1978 after I suspected that the visits were leading to increased predation, a hypothesis also suggested by Bart (1978). The numbers of eggs laid, eggs hatched, and nestlings were recorded at each visit. If the nest had been deserted, any remaining young were weighed, preserved, and deposited in the Royal Ontario Museum in Toronto, Ontario.

Nest Habitat

Smith (1976) postulated that dominant birds may be able to secure higher quality nesting territories than subordinate birds. Coulson (1968) and Smith (1976) have demonstrated that dominance status affects territory quality in a non-passerine and passerine respectively. Extending Smith's suggestion to this study, that dominant birds nest in higher quality habitat than subordinates, I predicted that brightly- or red-coloured birds would nest in higher quality habitat than pale or white-coloured birds. Although

habitat quality as judged by a bird is difficult for a human to assess, the prediction would be confirmed if habitats chosen by red birds (those with highest nesting success if the previous prediction is upheld) were similar to each other and differed from habitats in which pale birds (those with low-predicted nesting success) nested.

In order to test this prediction I used James and Shugart's (1970) method to obtain a quantitative description of the habitat surrounding each nest. The 0.1-acre circular plot method (Lindsey, Barton and Miles 1958) provides easily measured estimates of tree density and dominance (basal area), shrub density, ground cover, canopy cover, canopy height and the number of tree, shrub and ground species. The 400 m^2 area they suggested sampling was reduced to a 25 m^2 circular plot of radius 2.82(±5 cm) centred on each nest. Since redpolls are not territorial do not feed in the vicinity of the nest, and frequently had nests located within a few metres of an adjacent habitat-type, I felt an area as large as 400 m^2 was unnecessary and could misrepresent the habitat in which the nest was actually situated.

In order to provide a simple, two-dimensional description of the similarity of habitats (based on measurements taken) in which Inuvik and Krekovick Landing nests were found, each was re-expressed by means of reciprocal averaging ordination. Hill (1973) described this technique which uses successive calibration of variables and

then nests, to arrive at a unique and objective solution. Eigenvectors are extracted from the data by a method similar to principal components analysis. Reciprocal averaging has several advantages in that it provides an ordination of plots and variables, the optimal solution is arrived at without researcher bias and the technique distorts data less than some other ordination techniques (Gauch, Whittaker and Wentworth 1977). Applying the reciprocal averaging technique to Inuvik and Krekovick Landing nests (the two sites were treated separately), I obtained graphs illustrating the positions of nests along the first and second eigenvectors. Beside each respective nest on the graphs, were added the plumage colour scores of parents and their nesting success to determine if successful and/or nests of red birds were grouped in a particular habitat-type apart from less successful and/or nests of pale birds.

Nest Defense

Grinnell (1947), Clement (1968) and Newton (1972) reported on anecdotal evidence, that redpolls exhibit no territorial defense. I decided to test this because territoriality is important to the status signalling hypothesis. In order to test if redpolls defended territories, models were placed close to nests (Lack 1946, Siglin and Weller 1963, Blurton-Jones 1968) at Krekovick Landing in 1978. I also wished to see if the colour of the model (or interloper) affected the reaction of nesting parents. For example, a red-breasted interloper might be

more threatening and therefore invoke a greater response than a white-breasted interloper as Lack (1946) observed in European Robins (*Erithacus rubecula*).

The two models I used were made of stuffed skins of male redpolls caught at Krekovick Landing just prior to the experiments. One of the birds caught had a white breast (scored 0), the other's entire breast was red (scored 5). A matchbox fitted with a head made of clay (two black pins serving as eyes were the only features on the head) functioned as a control. The two models and the control were each tested at three stages of nesting of redpolls at the Landing, when eggs were present in the nest, shortly after the eggs hatched and just before the young were to fledge, except the white model and control which were not tested at the egg stage because of time contraints and the paucity of nests found at this stage.

Before the model was positioned at a nest, the nest was observed for one to three hours in order to establish the pattern of attendance by the parents. The model was then attached to a branch within 20 cm of the nest so that it appeared to be perching on a branch, looking toward the nest. After the model was fixed near the nest, the reaction of the parents returning to, and then attending, the nest was observed for one to two hours. Thus the nests were observed for a total of two to five hours.

D. Behaviour

General

The crucial prediction of Rohwer's status signalling hypothesis is that plumage colouration predicts social status in a dominance hierarchy (Rohwer 1975). Because it was difficult to obtain extensive data on dominance relations of wild redpolls, I conducted experiments with captive birds that would test this prediction. The experiments afforded two tests of Rohwer's hypothesis. First, Rohwer's prediction that brightly coloured birds would dominate pale birds in hierarchies was tested with observations of the agonistic behaviour of captive birds whose colour could be accurately measured. Secondly, Rohwer (1977) predicted that subordinates should defer to artificially brightened birds, who should be persecuted by dominant birds perceiving an incongruence between the signal (plumage colour) and behaviour of the colour-enhanced bird. This prediction was tested by artificially colouring a randomly-chosen individual midway through each experiment and observing any changes in the behaviour of all birds in the hierarchy.

Eleven experiments with six captive birds each (seven in the first experiment) were conducted in 1978 and 1979, seven in winter-spring, four in summer. Test birds were mist-netted immediately prior to each experiment, except in three of the summer experiments when they were captured one to three weeks before the experiments and were kept in

several small holding cages. At the time of capture the birds' weights and external body measurements were taken and plumage colour was scored. Birds were color-banded on each leg, one colour per bird in the experiment. The six birds chosen for an experiment were either those available at the time, or if more than six birds were caught, individuals with a wide range of breast colouration were picked. When birds were held prior to experiments, those not kept together were used. Six birds were used in two successive experiments because a sufficient number of new birds were not available. Sex and age were determined by autopsy after experiments. Although bands were difficult to see at times, particularly when it was very cold, I rejected a more obvious identification mark, such as a coloured feather attached to the retrices (Hammerstom 1942), to avoid possible effects of such on behavioural interactions. A summary of birds used in experiments is in Appendix 1.

An aviary, of volume 7.8 m^3 (2.4 m tall by 1.8 m wide and 1.8 m deep), located in Parkland County, Alberta, was used for winter experiments. In summer, an aviary approximately 6.6 m^3 (2.1 m wide, 1.5 m deep, 2.1 m high at the front and 1.5 m high at the back), occupied one half of a garden shed that was situated on the grounds of the Inuvik Research Laboratory. Thus each bird had an average of 1.3 m^3 of space in winter or 1.1 m^3 in summer, that was much larger than space alloted for birds in other aviary studies (e.g. Dilger (1960) allotted 0.04 m^3 per redpoll; Thompson (1960)

allotted 0.4 m^3 per House Finch; Tordoff (1954) provided 0.8 m^3 per Red-winged Crossbill (*Loxia leucopter*)).

The winter aviary was built adjacent to the west wall of a house. Plastic screening covered three sides and the top of the aviary while the house formed the fourth side. Commercial finch seed mixture and "budgie" gravel were given to the birds *ad libitum*. They obtained water from snow when it was present; otherwise a shallow container filled with water was provided. Two young poplar trees within the aviary provided perches and roosting places. Two windows faced directly into the aviary and provided an observation point.

The summer aviary was partially protected from ambient weather conditions. Aluminum screening covered the wall partitioning the aviary and observer halves of the shed and 1 m of the front of the aviary; the walls and roof of the shed enclosed the remainder. The doors of the shed facing the west were kept open, so that the temperature in the aviary approximated ambient temperature, but light levels were lower than ambient and shelter was provided from most precipitation and wind. The observer sat about 1 m from the screen in the other half of the shed. Proximity of the observer did not seem to affect the birds, a point also noted by Dilger (1960) for redpolls. Commercial finch seed mixture and "budgie" gravel were abundantly sprinkled on the floor of the aviary and fresh water was supplied daily. Alder and willow bushes and spruce saplings were freshly cut for the aviary at the commencement of each experiment.

The birds were observed daily for varying lengths of time. The average length of an experiment was 10 days and 32.4 hours of observation. Every three days the birds were weighed. After a hierarchy was established one randomly chosen bird was coloured red. Red hair dye applied to the bird's breast, rump and cheeks was used in the first five experiments. In six experiments a red histological dye (Ponceau-Acid Fuchsin) was used as the colouring agent, and another bird, randomly chosen from the remaining five uncoloured birds, was coloured green with a histological dye (Light Green) as a control (Marler 1955b).

At the time of colouring, all birds were removed from the aviary, weighed and then the four or five untreated birds were re-introduced. From 30 to 60 minutes were required to apply the colouring agent and allow the feathers to dry, after which time the treated bird(s) were returned to the aviary and observations were continued.

Table 1 lists the behaviours, originally described by Dilger (1960) for captive redpolls, that were recorded. Greatest emphasis was placed on recording agonistic encounters (those behaviours associated with attack and escape tendencies; Scott and Fredrickson 1951) that provided dominance-subordinance information. The initiator and its behaviour, the recipient of the behaviour and its reactions were recorded for each encounter. Numbers of agonistic encounters sufficient to determine dominance relations, were observed in each experiment without limiting food or

Table 1. Summary of behaviours recorded from observations of captive redpolls. These are based on Dilger's (1960) original descriptions.

Agonistic	
Avoidance	
	Head toward or approach opponent
	Head forward threat
	Head forward threat with gaping
	Head forward threat with wings raised
Attack	
	Chase
	Attack
Submissive	
	Retreat
Maintenance	
	Feeding or drinking
	General activity, i.e. flying
	Preen
	Rest
Courtship	
	Courtship Feeding

starving birds as Shoemaker (1939), Marler (1955a) and Dilger (1960) all did. All behaviours, and the time at which they occurred, were noted by hand.

Computations

Ranks

Following the general method outlined by Brown (1975) two dominance matrices were constructed for each experiment--one based on observations prior to artificial colouration, the other on observations after colouration. Each matrix contained frequencies of all encounters won and lost by each bird. A bird was considered dominant over another if, in encounters between the two, the number of wins exceeded the number of losses. The rank assigned to each bird was equal to the number of individuals a bird dominated. A bird that dominated five individuals (rank=5) was the alpha bird in the group, whereas a bird with rank 0 dominated no others and so was the omega bird in the hierarchy. Such a ranking system easily accommodated ties and triangles in the hierarchy since the numerical value of the rank did not imply a unique position in the hierarchy.

Behaviour Scores

Because the complexity of the birds' behaviour was not adequately described by each bird's rank alone (Collias 1950), behavioural scores were computed for each individual in each experiment. The number of agonistic encounters initiated, the number won (regardless of who initiated the encounter) and the total number of agonistic encounters in

which an individual participated per 10 hour period were tallied for each bird before and after the time of artificial colouration. The 10 hours were randomly chosen from observation times during which the rate of aggressive encounters was homogeneous (Marler 1955a; see below, Rates of Aggressive Interaction). Attacks and chases, hereafter referred to as attack behaviour, were separated in these tallies from the remaining agonistic behaviours which are referred to as avoidance behaviour (see Table 1).

Four behavioural indices were derived from the three scores described above. The first (number of encounters won divided by the number of encounter participated in), is a measure of the position of an individual in a hierarchy and may be loosely taken as dominance (Fretwell 1969, Baker and Fox 1978); a bird who won all encounters in which it participated would have a score of 1 whereas a bird that lost all encounters in which it participated would have a score of 0. The second index (number of encounters won divided by the number of encounters initiated) may be interpreted as the success of a bird in winning encounters it initiated. Values for this index typically ranged from 0.3 to 1.5. The third index (number of encounters participated in minus the number of encounters initiated) represents the number of aggressive attacks or threats a bird received, or to which it was victim. Thus the dominant bird would have a score of 0, and the omega bird, a score approaching the number of encounters in which it

participated. The last index (number of encounters initiated) is simply the number of encounters an individual initiated per 10 hour period and is considered a measure of the aggressiveness of that bird. The agonistic behaviour of every bird is therefore summarized by four values of each index (a total of 16 numbers for each bird): those calculated before and after artificial colouration took place, and for both avoidance and attack behaviours. The six birds used in two experiments were essentially treated as new birds in the second experiment. Thus, they had four values of each index that described their behaviour in the first experiment and four values of each index (independent of the previous set) for the second experiment.

Direction of Aggression

Rohwer predicted that most fights should occur between birds of similar plumage colouration, or that "likes-will-fight". This prediction was tested by two methods, based on the assumption that birds would be ranked in hierarchies according to their colour, as Rohwer predicted. First, the number of aggressive interactions each bird initiated towards the bird of immediately adjacent, lower rank and the omega bird (of farthest lower rank) were tallied (these scores could not be obtained for the lowest and second lowest birds in the hierarchy). The second method by which the prediction was tested was first used by Ketterson (1979a). The number of birds subordinate to an individual was divided into an upper half of those of nearby

rank, and a lower half of those of more distant rank. The number of aggressive acts directed towards each half was tallied. If the number of subordinate birds was odd, 50 per cent of the number of aggressive interactions involving the middle bird was added to the top half, and 50 per cent to the lower half. Counts from both methods were tallied before the artificial colouration for avoidance and attack behaviour separately. After colouration only scores computed by method 1 were calculated.

Rates of Aggressive Interaction

As birds were observed over various hours daily and during winter and summer, times when their activity levels varied considerably, their rates of encounter were examined in order to determine the hours during which their activity was relatively homogeneous. The number of all aggressive encounters in the hierarchy (of avoidance and attack behaviours combined) was averaged for each hourly interval and every average hourly rate had an associated standard deviation. A scattergram of aggressive interactions per hour against hour (Figure 3) showed distinct winter and summer groups. The results of a weighted covariance analysis with season as covariate and the standard deviation of each average as its weight (Table 2) were highly significant; the means and slopes of the two seasons were significantly different from each other and the covariate was signficantly different from zero. A test of significance of each weighted regression alone yielded significance for the summer group

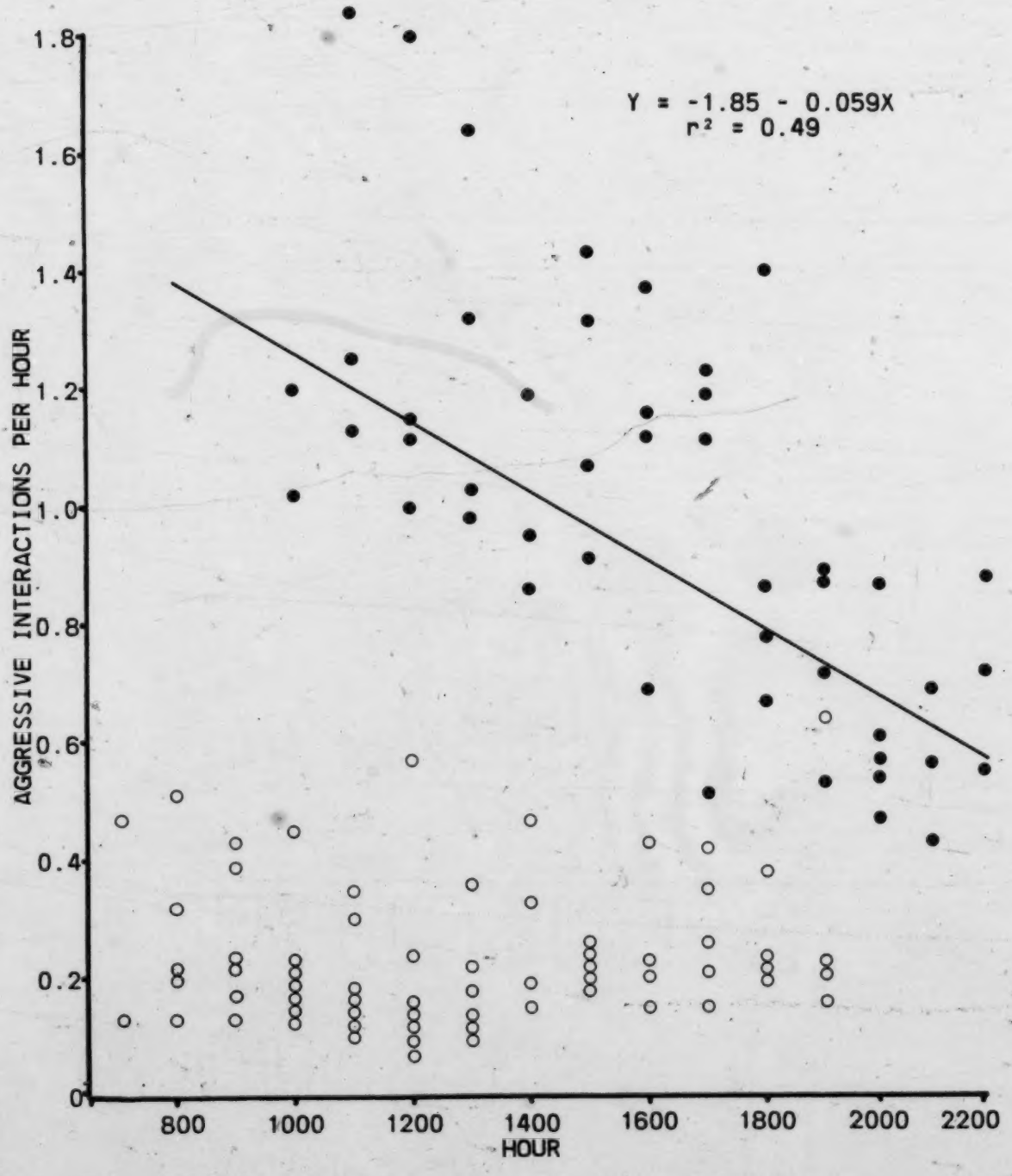

Figure 3. Graph of the relationship between hourly rates of aggressive interactions and hour of day that captive redpolls were observed. Line was fitted from least squares of weighted regression. The weight applied was the standard deviation associated with each point. Closed circles represent summer rates, open circles represent winter rates.

Table 2. Results of a weighted covariance analysis of hourly rates of aggressive encounters on hours during the day that redpolls were observed. The covariate used was season and the weight was the standard deviation associated with each rate of encounter.

Test	Value	df	F	P
Beta				
covariate=0	covariate=-0.02	1,108	14.00	<0.001
winter=summer	winter= 0.003 summer=-0.059	1,107	33.81	<0.001
Mean				
winter=summer	winter=0.21 summer=1.04	1,108	308.12	<0.01

only; thus the rate of aggressive interaction declined throughout the day in summer, but remained constant in winter. The summer observations appeared to be disjunct at 1700 hours. The mean rate from 0900 to 1700 hours was significantly greater than the mean rate from 1700 to 2400hours ($t=5.17$, $df=42$, $p<0.005$). Since the birds often rested from 1700 to 2400 hours, behaviour scores were taken from observations between 0900 and 1700 hours when they were more active.

E. Analysis

Data not normally distributed were tested with nonparametric procedures such as the Sign Test, Wilcoxon Signed Rank Test, Mann-Whitney U Test and Kruskal-Wallis One-way Analysis of Variance (Siegel 1956). A one-sample Kolmogorov-Smirnov test was used to test the normality of variable distributions and regression residuals. Where the data were normally distributed or a transformation applied to the data brought the distribution close to normality, I used parametric statistics such as regression (univariate, step-wise multiple and multiple multivariate; Neter and Wasserman 1974), and canonical variates analysis (Morrison 1967). A probability level of 0.05 was considered statistically significant for all tests. Programmes from the Biomedical Computer Programs P-Series (Dixon and Brown 1979) and programmes written by Dr. D.L. McLeish in APL were used for the analyses.

V. RESULTS

A. Breeding

Nesting

The most direct test of the application of the status hypothesis to the breeding season is to compare the reproductive success of birds differing in colour: red birds should enjoy greater reproductive success than pale birds. Contrary to the predicted outcome, clutch size at each location, number of eggs hatched and the number of young fledged did not differ among males of different breast colours attending nests at Inuvik and Krekovik Landing (Table 3).

Alternatively, I tested the hypothesis that larger birds (those presumed to be dominant) are reproductively more successful than smaller birds (those presumed to be subordinate). In this case size was estimated by six external body measurements. Hoary-type males attending nests containing a clutch size of four eggs were significantly larger than those attending nests with five eggs (Hotelling's T^2, $F(6,2)=20.10$, $P=0.05$; common- and hoary-type fathers were separated for this analysis because their body measurements differed significantly from each other (Hotelling's T^2, $F(6,10)=3.45$, $P=0.04$)). The size difference may be an artifact of the small sample size. Common-type males attending nests with four eggs and five eggs were similar in size as were parents of either type in

Table 3. Comparison of nesting success (mean±S.E.) according to breast colour of males by means of Kruskal-Wallis One-way Analysis of Variance (df=2). Breast colour categories are white (subjectively assigned scores 0 and 1), pink (2 and 3) and red (4 and 5).

Stage	Breast Colour			N	H	P
	White	Pink	Red			
Eggs laid						
Inuvik	5.0±0	4.8±0.2	4.0±0	8	3.27	0.19
Krekovick	4.3±0.3	4.5±0.3	4.0±0	9	1.33	0.51
Eggs hatched	4.0±0.3	4.1±0.2	2.5±1.5	15	1.92	0.38
Young fledged	3.0±0.4	1.3±1.3	1.0±0	8	1.78	0.41

relation to the number of their eggs that hatched.

The body measurements of pairs of birds were compared to determine if a pattern existed within pairs, i.e. large birds with large mates, large with small, etc. A canonical correlation analysis and a multivariate regression of the body measurements of mated pairs were both non-significant. Similarly, there was no apparent pattern between the breast colours of mated pairs. Frequencies of breast colours (numbers of birds lacking red breast colour, those with pink breasts and those with red breasts) among males known to be mated was similar to those of all males banded during the breeding season (Figure 4; commons, n=82, chi-square=4.71, df=5, P=0.88; hoaries, n=27, chi-square=0.02, df=2, P=0.88). These results suggest that choice of mates was random.

Nesting Habitat

The generally accepted idea that dominant individuals fare better than subordinates in winter hierarchies was extended to the breeding season by Smith (1976). She predicted that dominant birds should acquire higher quality territories than subordinates and offered as evidence work by Coulson (1968) on a non-passerine, several studies reviewed by Watson and Moss (1970), and her work on chickadees (Smith 1976). Weatherhead and Robertson (1977) and Plesczyznska (1978) demonstrated a positive correlation between territory quality and individual 'fitness in passerines. On the basis of Smith's work, I hypothesized that red birds (predicted to be dominant) should nest in

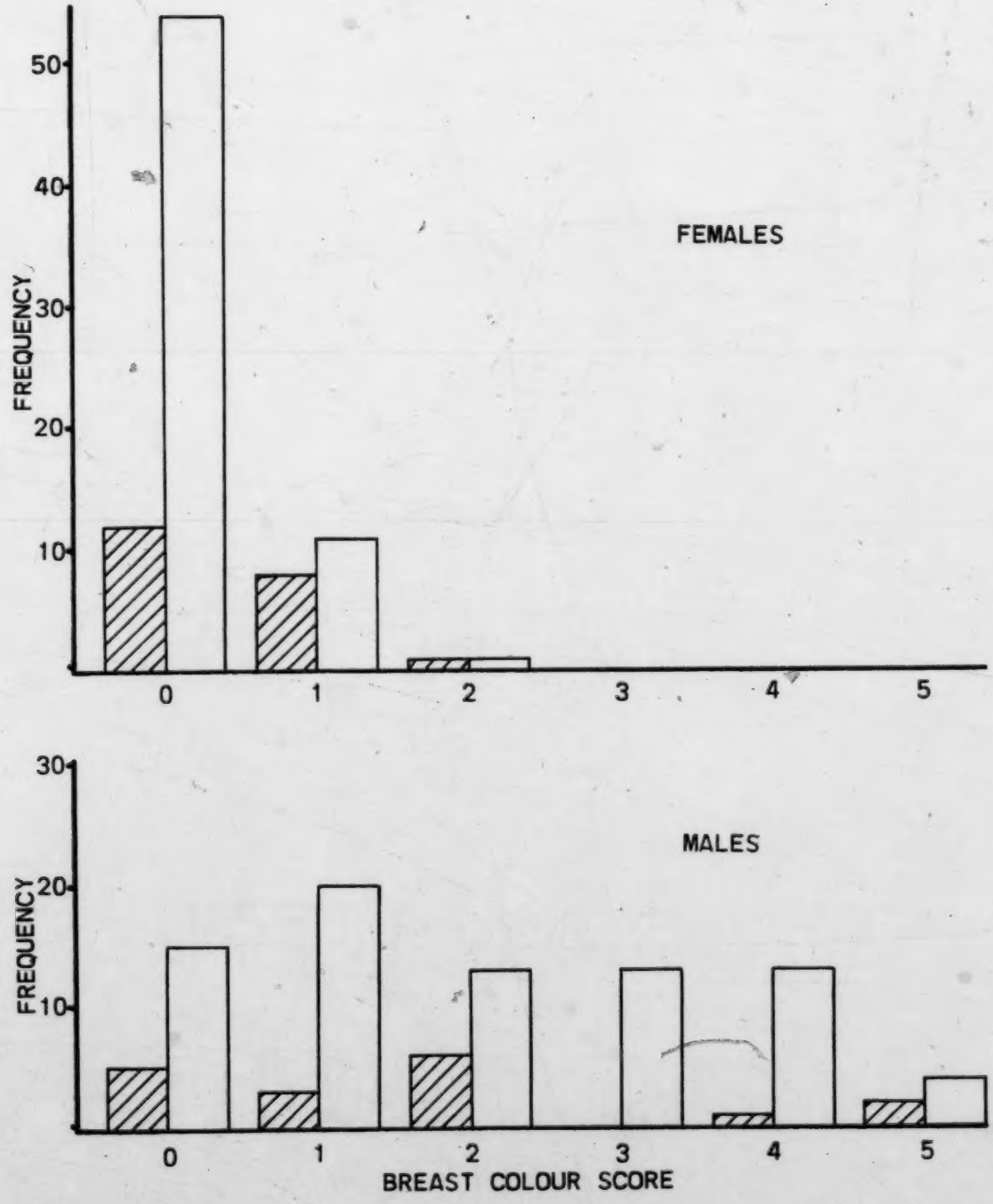

Figure 4. Frequency distribution of breast colour scores of birds known to be mated (hatched bars) and all other birds (open bars) netted during summer at Inuvik and Krekovick Landing.

better habitat than pale (predicted to be subordinate) birds. Although territory quality is difficult to assess, my prediction would be at least partially confirmed if all red birds nested in similar habitat that differed from that in which pale birds nested. In my study, habitat quality was described by variables characterizing the vegetation around the nest (for example, tree density and height), and the position and location (in terms of habitat-interfaces) of the nest. Reciprocal averaging ordination was used to provide a visual summary of the positions of nests with respect to each other, according to the vegetation and nest variables measured (Inuvik and Krekovick Landing nests were treated separately because of major vegetation differences--open boreal forest vs tundra respectively). Contrary to the prediction, an examination of the ordinated nests, that took into account the colouration of parents and nesting habitat, showed that nests of red birds were not separated from nests of pale birds, in either Inuvik or Krekovick Landing (Figure 5). Nest ordinations, which considered clutch size and number of eggs hatched, showed that the nest habitat was not related to nesting success.

Inuvik nests were ordinated on the first reciprocal averaging axis according to decreasing shrub density, and frequency of small trees, and increasing frequency of moderate and large-sized trees (from left to right, Figure 5, top). On the second axis, the habitats in which nests were found were positioned in terms of increasing tree

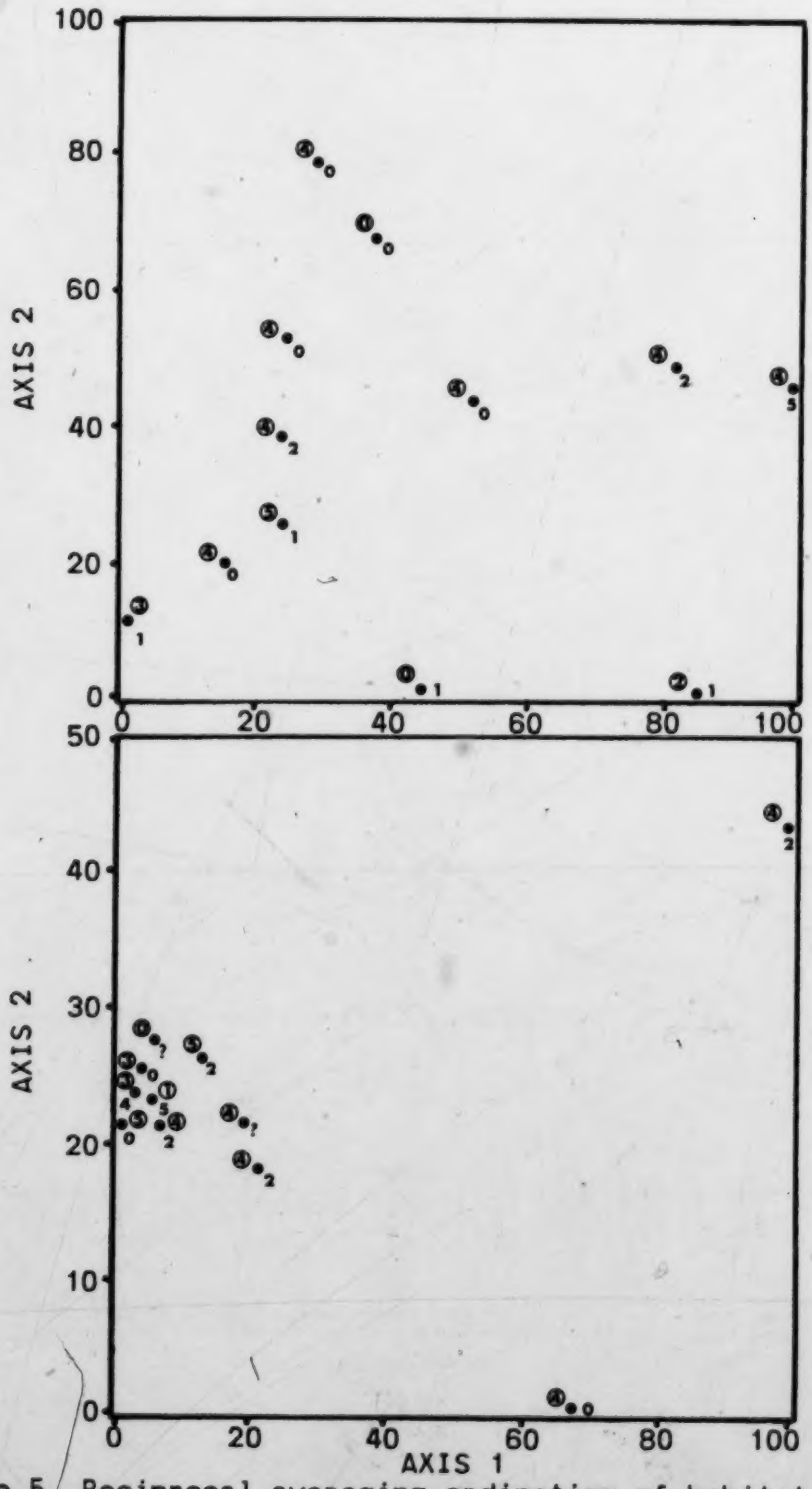

Figure 5. Reciprocal averaging ordination of habitats in which redpoll nests were found at Inuvik (top) and Krekovick Landing (bottom). Axes are described in text. Numbers not in circles represent breast colours of males attending nests; numbers in circles represent clutch sizes.

density and abundance of White Spruce, and decreasing canopy cover, frequency of large trees and height at which the nests were built (from bottom to top). Krekovick Landing nests were ordinated on axis 1 according to increasing shrub height, and decreasing shrub density, ground cover and number of herbaceous species found (from left to right Figure 5, bottom). The trends illustrated on axis 2 were an increase in the percentage of the herbaceous community dominated by one species, a decrease in nest height and a shift from nests located in homogeneous vegetation to those located juxtaposed by different vegetation-types (from bottom to top).

Nest Defense

Seven experiments which involved either stuffed and mounted redpolls or a control at a nest, were conducted for two purposes: first, I wanted to test the supposition that redpolls are not territorial (Grinnell 1947, Clement 1968, Newton 1972) and secondly, to determine whether the parents reacted differently to a red-breasted model than a white-breasted one. I observed either little or no reaction of parents towards models at nests and I could detect no differences in reaction according to the nesting stage at the time of the experiment or the model used. In most cases one or both parents returned to their nest at a predictable time (based on observations made immediately before the model was introduced), and their activities were unaffected by the foreign object. Models were lightly pecked in three

out of seven experiments (the white-breasted model at a nest containing eggs, the red-breasted model at a nest with young approximately three to five days old, and the control at a nest containing recently hatched chicks). The control stimulated the greatest response of any of the models, but even that reaction was modest in contrast to accounts given by Lack (1946) of the reaction of nesting European Robins to a stuffed robin.

Successive experiments with different models were conducted at two nests six and nine days apart, because of the few nests available for testing. On the first occasion both pairs of birds hopped around and gently pecked at the models (this accounts for two of three observations in which a reaction to a model was noted); the second time they took no notice of the models. Thus, apparent habituation of these parents to models may have been responsible for the lack of response on the second occasion.

These experiments did reveal variability in the attentiveness of parents. Those parents that left the nest unattended for varying lengths of time, visited the nest without their mate and generally took little notice of models fixed by their nest, differed from others that closely attended the nest, often visited with their mate, tended to vocalize in response to intruders and strike a model placed in proximity to their nest. The parents' reactions to models were similar to their behaviour when I inspected nests or caught parents for banding. These results

agree with reports of considerable individual variation in reactions of birds to models or of attentiveness to nests (e.g. Lack 1946, Blurton-Jones 1968).

B. Behaviour

The following general aspects of the dominance behaviour of redpolls were noted from my observations of captive birds in experiments. Dominance-subordinance relationships, often in the form of subtle agonistic behaviours such as supplants, were easily discernable in all captive experiments. Three of the seven hierarchies observed during winter were non-linear: one of the three had six non-linear relationships out of a possible 15 unidirectional pairs, the other two had three. Of the four hierarchies observed during summer one had one non-linear relationship. These observations are at variance with Dilger's (1960) report of a strict linear hierarchy which was established within three days by the captive redpolls he observed.

By far the most common agonistic behaviour in these experiments was one bird supplanting another individual which in turn usually retreated. Dominant birds supplanted subordinates at food sources, roosting positions and at times in an apparently random fashion. Attack encounters occurred with frequency only during summer experiments. The ranks and behaviour scores of the six birds used in two experiments were not significantly different in the second

experiment than in the first.

Since winter and summer values of two of the four behaviour variables (victim and aggressiveness) were signficantly different (Table 4), data from winter and summer experiments were analyzed separately. Individuals' avoidance scores were not highly correlated with their attack scores (Table 5) so these too were analyzed separately. Hoary-types tended to dominate and be more aggressive than common-types in experiments during winter (Table 6).

Males were significantly more dominant than females during summer, and were more successful at winning agonistic encounters than females during winter (Table 7). However, the method used to analyze dominance relations between sexes influenced the interpretation of the results. When dominance relations of all bisexual pairs within an experiment were examined, males dominated females about two-thirds of the time (24 out of 35 pairs during the winter, 23 out of 33 during the summer). Yet, during both seasons birds' ranks were independent of their sex (winter, chi-square=1.81, df=5, P=0.85; summer, chi-square=6.26, df=5, P=0.20).These results indicate that males tended to dominate females but this was not steadfast as Dilger reported for redpolls, and Marler (1955a), Hinde (1955, 1956), Thompson (1960), Coutlee (1967) and others reported for other cardueline finches. These authors observed that females became dominant over their mates during summer. In my experiments dominance

Table 4. Comparison of winter and summer avoidance behaviour scores (mean±S.E.) by means of Mann-Whitney U test, with sample size of 41 for winter and 24 for summer.

Variable	Winter	Summer	U	P
Dominance	0.46±0.05	0.47±0.06	507	0.83
Success	0.99±0	0.92±0	549	0.43
Victim	21.54±2.85	94.99±10.74	104	<0.01
Aggressiveness	21.02±3.22	90.62±13.53	172	<0.01

Table 5. Results of multivariate multiple regression analysis of attack on avoidance behaviour scores, with 1 and 19 df.

Dependent variable	F	P	R^2	Beta
Dominance	30.18	<0.01	0.61	0.95
Success	0.56	0.46	0.03	0.30
Victim	6.50	0.02	0.25	0.16
Aggressiveness	2.43	0.13	0.11	0.15

Table 6. Comparison of behaviour scores (mean±S.E.) of common and hoary-type redpolls by means of Mann-Whitney U test with sample sizes of 30 and 10 for winter, 11 and 13 for summer, common and hoary respectively.

Variable		Common	Hoary	U	P
Dominance					
avoidance	winter	0.40±0.05	0.64±0.07	82	0.03
	summer	0.44±0.10	0.49±0.08	65	0.71
attack	summer	0.37±0.11	0.48±0.10	36	0.18
Success					
avoidance	winter	1.00±0.04	1.02±0.01	100	0.09
	summer	0.91±0.05	0.93±0.06	50	0.21
attack	summer	0.91±0.10	0.97±0.03	56	0.90
Victim					
avoidance	winter	23.75± 3.60	15.70±11.33	184	0.28
	summer	106.09±20.40	85.61± 9.94	89	0.30
attack	summer	18.91± 5.14	17.08± 4.32	62	0.60
Aggressiveness					
avoidance	winter	19.84± 4.18	25.80± 3.41	91	0.06
	summer	78.00±15.58	101.31±21.34	62	0.60
attack	summer	21.91± 3.74	23.00± 9.41	46	0.52

Table 7. Comparison of behaviour scores (mean±S.E.) of male and female redpolls by means of Mann-Whitney U test with sample sizes of 29 and 9 for winter, 15 and 9 for summer, male and female respectively.

Variable		Male	Female	U	P
Dominance					
avoidance	winter	0.48±0.06	0.42±0.09	120	0.73
	summer	0.55±0.08	0.34±0.09	97	0.08
attack	summer	0.52±0.09	0.29±0.12	49	0.73
Success					
avoidance	winter	1.02±0.04	0.94±0.03	184	0.05
	summer	0.94±0.04	0.89±0.08	61	0.70
attack	summer	0.97±0.02	0.97±0.17	47	0.82
Victim					
avoidance	winter	21.10± 3.88	21.91± 4.14	107	0.42
	summer	84.33±13.99	112.78±15.58	47	0.23
attack	summer	17.00± 3.90	19.44± 3.03	38	0.58
Aggressiveness					
avoidance	winter	20.83± 3.43	23.82± 8.95	111	0.50
	summer	111.67±17.95	55.56±14.72	103	0.03
attack	summer	25.07± 8.05	7.22± 2.76	55	0.43

reversal with season was probably not observed because I did not observe the same birds in both season.

Behaviour and Colour

The definitive test of the status signalling hypothesis is to determine if the behaviour of individuals in a hierarchy could be predicted by their colour. In the experiments I conducted the ranks of birds were independent of their breast colouration (winter, chi-square=8.18, df=10, P=0.60; summer, chi-square=6.77, df=4, P=0.16). Similarly, there was little relationship between a bird's behaviour and its breast colouration as described by the trichromatic coefficients. This held for both avoidance and attack encounters, and for common- and hoary-type redpolls in multiple multivariate regressions with and without a covariate for season (Table 8) and multiple step-wise regressions (Table 9). Scatterplots of the data (Figure 6 illustrates two of the variables, dominance vs dominant hue), and tests of the regression residuals for normality confirmed that higher order regression models were unnecessary and illustrated the randomness of the relationships. For those models in which the F-ratio of regression mean square to error mean square was significant (an indication that the slope(s) are not equal to zero), the coefficient of multiple determination was, nevertheless, close to zero. Values close to zero result when independent variables contribute little or nothing to the prediction of dependent variable(s). These results clearly demonstrate

Table 8. Results of multiple multivariate regression of behaviour scores on breast colouration variables with 4 and 46 df for avoidance scores and 4 and 12 for attack scores.

Dependent Variable	Multiple R^2	F	P
Dominance			
avoidance	0.19	2.74	0.04
attack	0.43	2.29	0.12
Success			
avoidance	0.09	1.08	0.38
attack	0.15	0.55	0.70
Victim			
avoidance	0.13	1.79	0.15
attack	0.08	0.27	0.89
Aggressiveness			
avoidance	0.04	0.48	0.75
attack	0.21	0.79	0.55

Table 9. Results of step-wise multiple regressions of avoidance behaviour scores on breast colouration variables. Independent variables are listed in the order of inclusion in the regressions. The R^2 represents a cumulative value. Criterion for inclusion of an independent variable was F=4.0 and removal F=3.9.

Dependent Variable	Independent Variables	F	df	P	R^2	Beta
Dominance	Brightness	10.73	1,50	***	0.18	0.04
	Red	1.22	2,49	NS	0.20	-2.93
Success	Red	1.78	1,49	NS	0.03	0.23
	Purity	1.69	2,48	NS	0.07	-1.64
Victim	Red	3.86	1,50	NS	0.07	-186.49
	Hue	1.66	2,49	NS	0.10	-432.38
	Brightness (Red removed)	6.23	2,49	***	0.11	1.95
Aggressiveness	No variables					

*** P<0.001

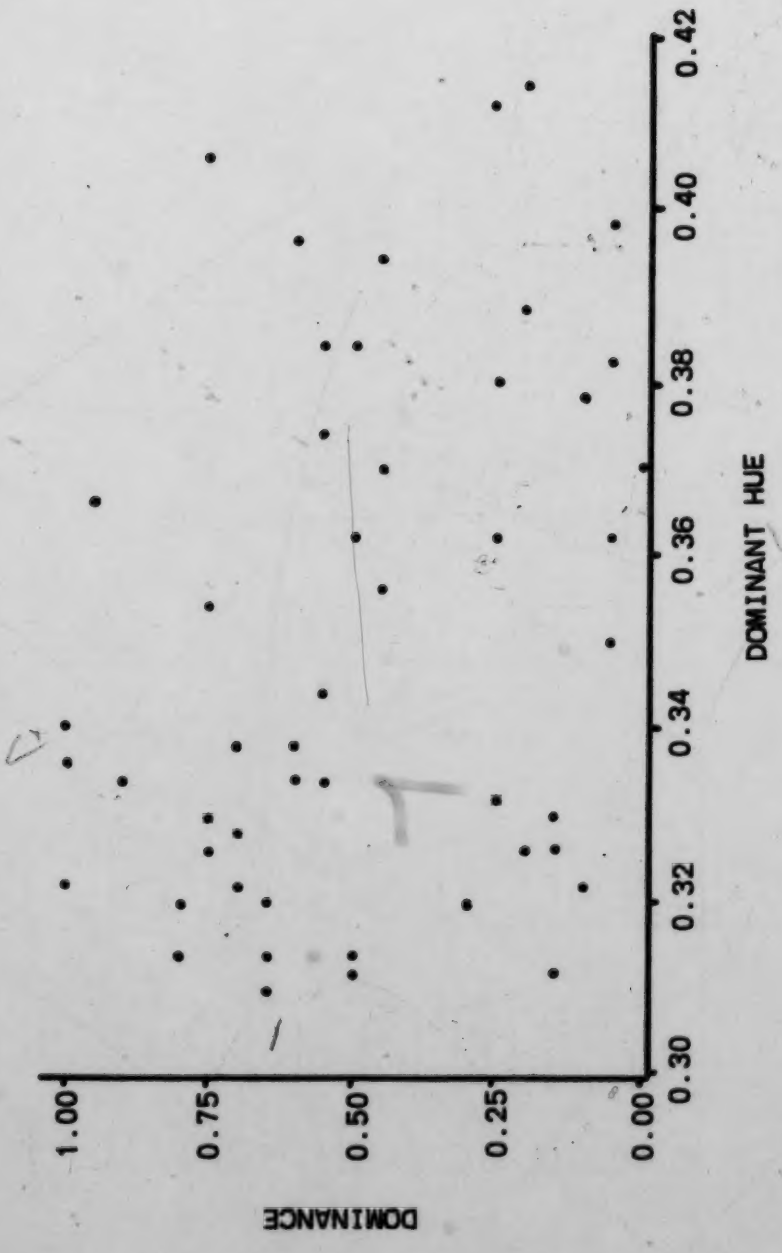

Figure 6. Graph of the relationship between dominance scores and dominant hue of captive redpolls.

that behaviour was independent of colour, contrary to the predicted outcome.

Artificial Colouration

Rohwer (1977) predicted that individuals whose colour was artificially enhanced would be deferred to by birds of lower-signalled rank (pale birds) and persecuted by those of higher signalled rank (brightly coloured birds). Although my data suggest artificially coloured birds changed rank more often than birds not artificially coloured as predicted, the difference was not significant (chi-square=2.80, df=1, P=0.09). Eleven changes in hierarchical ranking were observed in all 67 birds, 5 of which were among the 17 birds artificially coloured (2 out of 6 coloured green, 3 out of 11 coloured red). All changes were to either an adjacent higher or lower rank--no bird changed rank by more than one position.

The behaviour of all individuals in the experiments did not differ significantly before and after the colouration of test birds for avoidance or attack interactions, or in winter or summer experiments, with the exception of one case as illustrated in Table 10. Seasons were treated separately because two variables had significantly different variances although the means for all variables were similar. The exception was in the victim index of attack encounters, which was significantly lower after colouration than before.

Artificial reddening of test birds did not affect their avoidance behaviour scores after treatment (Table 11).

Table 10. Comparison of behaviour scores (mean±S.E.) of all captive birds before and after artificial colouration by means of Student's t and Hotelling's T^2 tests with 42 df for winter and 23 for summer.

Variable		Before	After	t	P
Dominance					
avoidance	winter	0.46±0.05	0.49±0.05	-1.53	0.13
	summer	0.47±0.06	0.49±0.07	-0.66	0.52
attack	summer	0.43±0.07	0.45±0.07	0.01	0.94
Success					
avoidance	winter	0.99±0.03	0.96±0.03	-0.27	0.79
	summer	0.92±0.04	0.91±0.05	0.18	0.86
attack	summer	0.94±0.05	0.96±0.09	0.06	0.81
Victim					
avoidance	winter	21.53± 2.85	21.05± 2.42	0.24	0.81
	summer	95.00±10.74	84.08±10.92	1.42	0.17
attack	summer	17.92± 3.25	6.87± 2.03	7.11	0.01
Agressiveness					
avoidance	winter	21.02± 3.22	20.74± 2.54	-0.65	0.52
	summer	90.62±13.53	79.71±13.09	0.62	0.54
attack	summer	18.37± 5.38	7.37± 2.43	3.42	0.08

Hotelling's T^2		df	F	P
avoidance	winter	4,39	0.90	0.47
	summer	4,20	0.87	0.50
attack	summer	4,20	2.02	0.13

Scores of attack encounters of reddened birds were not analyzed statistically because there were too many scores of zero caused by the lack of attack behaviour during winter, but the scores tended to be higher before than after reddening. Scores of control birds that were coloured green, were similar before and after treatment. The victim index of reddened birds remained virtually unchanged before and after colouring. The scores presented here are directly analagous to, although more comprehensive than, data Rohwer (1977) presented on the effect of colour enhancement of Harris' Sparrows. Contrary to my results, his data showed that after colouration test birds received significantly more overt attacks (as compared to avoidance encounters) than prior to colouration.

Direction of Aggression

Based on the observation that more brightly-coloured birds dominated pale birds, Rohwer (1975) predicted that in the linear hierarchies of Harris' Sparrows most fighting will occur between birds of like plumage and hence status.He interpreted such fighting ("likes-will-fight") as disputes over rank rather than attempts to expel low ranking birds as in despotic fighting. Because the assumption that colour is correlated with rank was not met in redpolls, Rohwer's prediction that "likes-will-fight" becomes irrelevant in terms of the status signalling hypothesis.

Examination of aggressive interactions in redpolls showed that the agonistic behaviour of all birds was more

Table 11. Comparison of avoidance behaviour scores (means±S.E.) of artificially reddened birds before and after colouration by means of Wilcoxon Signed Rank test with 10 df.

Variable	Before	After	P
Dominance	0.34± 0.09	0.34± 0.09	0.65
Success	0.99± 0.12	0.81± 0.12	1.00
Victim	57.18±19.78	61.00±19.79	0.72
Aggressiveness	38.91±15.72	32.64±10.82	1.00

often directed toward birds of adjacent lower rank rather than toward the omega bird (Table 12a), thus confirming that disputes among captive redpolls serve to establish rank rather than eliminate subordinates. Dilger (1960) reported similar patterns of behaviour in captive redpolls. In both seasons and for both levels of aggression this tendency increased slightly following artificial colouration of test birds. The ratio of the number of attacks directed towards the bird of adjacent lower rank to the number of attacks directed towards the omega bird (aggression ratio 1) did not differ significantly when comparing the level of aggression, time in relation to the colour alteration, sex, season, species or rank (Table 12b). Thus, the distribution of agonistic behaviour was relatively constant throughout all experiments.

Generally the same results were obtained with the second method by which the direction of aggression was examined: the frequencies of agonistic behaviours directed towards the top half tended to exceed those directed towards the bottom half of a bird's subordinates (Table 13a). This difference was significant in the case of attacks during summer. The ratio of agonistic behaviours directed toward the top half to agonistic behaviours directed toward the bottom half (aggression ratio 2) did not change according to level of aggression, season, species or sex, but it did differ significantly with the rank of the birds (Table 13b).

The data illustrate that patterns of aggression of all

Table 12. Analysis of direction of aggression within hierarchies. Comparison of the number of encounters initiated by four top-ranking individuals with adjacent and omega individuals.

a. Comparison of aggression (mean±S.E.) directed towards adjacent or omega individuals. Test used was Wilcoxon signed Rank test with 25 df for winter and 16 for summer.

Comparison		Adjacent	Omega	P
Pre-colouration				
avoidance	winter	8.68±1.01	6.80±0.96	0.05
	summer	37.25±5.22	32.20±3.56	0.52
attack	summer	6.87±2.51	4.50±1.68	0.31
Post-colouration				
avoidance	winter	9.09±1.00	6.14±0.95	0.02
	summer	35.37±4.69	27.75±3.13	0.01
attack	summer	5.94±2.69	1.40±0.39	0.01

b. Comparison of aggression ratio 1 (see text) considering various factors. Two-way comparisons were made by means of Mann-Whitney U tests, multiway comparison was made with Kruskal-Wallis One-way ANOVA with 3 df.

Factor	Group	Mean±S.E.	N	P
Level of Aggression				
Pre-colouration	Avoidance	1.11±0.17	13	0.86
	Attack	2.02±0.90	13	
Post-colouration	Avoidance	1.33±0.15	9	0.31
	Attack	6.55±4.58	9	
Parts of Experiment	Pre-colouration	1.44±0.15	43	0.18
	Post-colouration	1.83±0.23	43	
Season	Summer	1.24±0.19	16	0.23
	Winter	1.80±0.29	29	
Species-type	Common	1.76±0.32	25	0.35
	Hoary	1.36±0.22	19	
Sex	Male	1.54±0.19	31	0.51
	Female	1.72±0.60	12	
Rank	5	2.04±0.33	8	0.18
	4	1.25±0.26	14	
	3	1.50±0.26	13	
	2	1.79±0.81	8	

Table 13. Analysis of direction of aggression within hierarchies. Comparison of the number of encounters initiated with the top and bottom halves of an individual's subordinates.

a. Comparison of aggression (mean±S.E.) directed towards top and bottom halves of an individual's subordinates. Test used was Wilcoxon Signed Ranks test with 25 df for winter and 16 for summer.

Comparison		Top	Bottom	P
Pre-colouration				
avoidance	winter	13.85±2.07	12.75±2.34	0.39
	summer	65.00±7.80	58.32±6.38	0.17
attack	winter	17.31±5.04	8.59±2.94	0.02

b. Comparison of aggression ratio 2 (see text) considering various factors. Two-way comparisons were made by means of Mann-Whitney U tests, multiway comparison was made with Kruskal-Wallis One-way ANOVA with 3 df.

Factor	Group	Mean±S.E.	N	P
Level of Aggression	Avoidance	1.16±0.11	16	0.06
	Attack	2.46±0.53	16	
Season	Summer	1.24±0.19	16	0.92
	Winter	1.80±0.29	29	
Species-type	Common	1.76±0.32	25	0.07
	Hoary	1.36±0.22	19	
Sex	Male	1.54±0.19	31	0.35
	Female	1.72±0.60	12	
Rank	5	2.04±0.33	8	0.03
	4	1.25±0.26	14	
	3	1.50±0.26	13	
	2	1.79±0.81	8	

birds at the beginning of experiments were exaggerated as time progressed; the ratio of aggression directed towards birds of neighbouring rank to birds of farther rank increased from the first part of the experiments to the second part (part corresponding to before and after artificial colouration of test birds). Tordoff (1954) and Ellis (1966) noted that the hierarchies of Red-winged Crossbills and Starlings (*Sturnus vulgaris*) respectively, became more rigid with time while retaining the same patterns. The tendency for more encounters between birds of close rank that I observed was also more pronounced with displays of overt aggression such as chasing and attacking than in avoidance situations, which indicates that birds of similar rank are more overtly serious opponents than birds of different rank.

Common-types engaged in aggression with birds of similar rank more than hoary-types (Tables 12b and 13b). This observation is consistent with higher dominance scores of hoaries, (particularly of avoidance interactions), as compared to commons: the greater the proportion of encounters an individual wins relative to those in which it participated (the definition of dominance used here), the less ambiguous is its rank and the less it needs to defend its position from rivals.

Behaviour and Morphology

Surprisingly, general body size, which was estimated by bill, wing, tail, and tarsus measurements, was poorly

correlated with behaviour scores. The relationship was tested with multiple multivariate and step-wise multiple regressions of avoidance and attack encounters during winter and throughout the year, and for common- and hoary-type redpolls (Table 14). Significant regression effects (i.e. significant F statistics) for victim and aggressiveness were found; however the coefficients of multiple determination were very low in the multiple multivariate regression (R^2=0.27 and 0.20 respectively). In both cases bill width was the only independent variable with a significant regression coefficient. In step-wise multiple regressions, each independent variable that met the criterion for inclusion in the model (F=4.0, a level commonly used; Dixon and Brown 1979), contributed very little to estimation of the dependent variable (Table 15). For example, bill width improved prediction of the victim index by only 10 per cent. Regardless of season, body weights of birds taken at the initiation of each experiment were not related to subsequent behaviour (Table 16). In fact, the two data sets were nearly independent with respect to each other, and in the cases of the victim index and aggressiveness regressions in which the F-values were significant, the reduction of variance attributable to weight was only eight and six per cent respectively.

There were no significant regression effects in a multiple multivariate regression of avoidance behaviour variables and skeletal measurements of birds tested (Table

Table 14. Results of multiple multivariate regression of behaviour scores on external body measurements with 6 and 58 df for avoidance scores, and 6 and 14 df for attack scores. Independent variables listed are those with Beta-values significantly different from zero as indicated by the t-values (df of t-values are 58 for avoidance scores and 14 for attack scores).

Dependent Variable	Multiple R^2	F	P	Independent Variable	t	P	Beta
Dominance							
avoidance	0.08	0.80	0.57	none			
attack	0.47	2.11	0.12	none			
Success							
avoidance	0.12	1.28	0.28	none			
attack	0.24	0.75	0.62	none			
Victim							
avoidance	0.27	3.61	0.00	Bill width	2.88	0.01	52.21
attack	0.14	0.37	0.89	none			
Aggressiveness							
avoidance	0.20	2.43	0.04	Bill width	3.62	<0.01	52.52
attack	0.29	0.98	0.48	none			

Table 15. Results of step-wise multiple-regressions of avoidance behaviour scores on external body measurements. Independent variables are listed in the order of inclusion in the regression. Criterion for inclusion of an independent variable was F=4.0 and removal F=3.9. The R^2 represents a cumulative value.

Dependent Variable	Independent Variables	F	df	R^2	Beta
Dominance	Tail	4.42	1,65	0.06	0.03
Success	Tail	3.73	1,63	0.05	0.01
	Tarsus	1.52	2,62	0.08	-0.03
	Bill width	1.35	3,61	0.10	0.08
Victim	Bill width	6.48	1,65	0.09	46.18
	Wing	5.69	2,64	0.17	-5.33
	Tarsus	3.99	3,63	0.22	12.28
	Bill length	1.48	4,62	0.24	-13.02
Aggressiveness	Bill width	13.01	1,65	0.17	65.98

Table 16. Results of univariate regressions of avoidance behaviour scores on body weight with 1 and 65 df.

Dependent Variable	F	P	r^2	Beta
Dominance	0.01	0.90	<0.01	-0.01
Success	0.01	0.94	<0.01	0.01
Victim	5.38	0.02	0.08	-11.70
Aggressiveness	3.89	0.05	0.06	-11.03

17; a regression with attack scores was not considered because of the large number of zero scores that resulted from the lack of attack behaviour during winter). In the multiple multivariate regression that was performed, the coefficients of multiple determination indicated that the skeletal measurements (independent variables) accounted for 49 to 73 per cent of the variance of the behaviour scores (dependent variables). The high R-values are likely an artifact of the large number of independent variables (19) included in the model (Neter, Wasserman and Whitmore 1978). This supposition was confirmed by step-wise multiple regressions; each skeletal (independent) variable reduced the variance of the dependent variable by only 5 to 10 per cent (Table 18). Exceptions to the low R-values were with scapular width and humerus length which contributed 20 and 33 per cent to the prediction of the victim index and aggressiveness respectively. The results of the numerous tests described here, demonstrate that dominance behaviour, both avoidance and attack, during summer and winter, was not significantly correlated with the morphological variables measured.

Table 17. Results of multiple multivariate regression of avoidance behaviour scores on skeletal measurements with 19 and 13 df. Independent variables listed are those with Beta-values significantly different from zero as indicated by the t-value (df of t-value is 13).

Dependent Variable	Multiple R^2	F	P	Independent Variable	t	P	Beta
Dominance	0.73	1.86	0.13	Scapular width	3.79	<0.01	0.02
Success	0.49	0.65	0.81	Keel length	2.50	0.03	0.003
Victim	0.64	1.23	0.36	none			
Aggressiveness	0.66	1.35	0.29	none			

Table 18. Results of step-wise multiple regressions of avoidance behaviour scores on skeletal measurements. Independent variables are listed in the order of inclusion in the regressions. Criterion for inclusion of an independent variable was F=4.0 and removal F=3.9. The R^2 represents a cumulative value. None of the independent variables were significant.

Dependent	Independent	F	df	R^2	Beta
Dominance	Keel length	3.41	1,32	0.11	0.003
	Hallux	4.24	2,31	0.20	-0.003
	Keel depth	1.70	3,30	0.25	-0.005
	Scapular width	5.04	4,29	0.36	0.02
	Humerus	4.38	5,28	0.45	0.004
	Tarsus	2.59	6,29	0.49	-0.003
	Premax. width	2.38	7,26	0.54	-0.003
	Coracoid	1.89	8,25	0.57	-0.002
Success	Premax. width	2.20	1,32	0.07	0.001
	Hallux	0.30	2,31	0.13	-0.001
Victim	Scapular width	8.02	1,32	0.20	-1.96
	Gonys	4.43	2,31	0.30	-0.57
	Furculum	7.76	3,30	0.44	0.31
	Keel length	1.34	4,29	0.47	-0.30
	Premax. length	2.68	5,28	0.51	0.42
	Sternum length	1.61	4,27	0.54	0.25
Aggressiveness	Humerus	6.39	1,32	0.33	1.25
	Femur width	3.91	2,31	0.41	-3.13
	Hallux	2.24	3,30	0.45	-0.76
	Furculum	2.31	4,29	0.53	-0.62
	Premax. length	2.00	5,28	0.56	0.68
	Lower man. width	2.79	4,27	0.54	0.40
	Scapular width	2.08	7,26	0.58	1.48

VI. DISCUSSION

The critical test of Rohwer's hypothesis is to determine if plumage colouration is strongly correlated with social status in a winter hierarchy. Secondarily, I have set out to determine if Rohwer's status signalling hypothesis could be extended to the breeding season, that is, if plumage colouration is directly related to reproductive success. Evidence from observations during the breeding season and from experiments are presented as tests of the hypothesis.

A. Observations

Rohwer (1975) did not extend his status signalling hypothesis to the breeding season but, if birds of high rank in winter hierarchies have a higher survival rate (Kluyver 1957, Lockie 1956), secure higher quality nesting areas and are chosen preferentially by females over low-ranking males (Smith 1976), then a logical extension of his hypothesis is that brightly-coloured, and hence dominant, males should have greater reproductive success than less brightly-coloured males. For example, Hogan-Warburg (1966) observed that dark-coloured Ruffs (*Philomachus pugnax*), defended territories and enjoyed preferential mating whereas Ruffs that were mostly white did not defend territories and often went unmated. The prediction is applicable to redpolls and other passerines which compete for resources through dominance hierarchies at some time during the year, exhibit

plumage variability, and molt just once a year after the breeding season. The first two conditions relate directly to those imposed by Rohwer. The last condition arises from Rohwer's assumption that the plumage colouration of species with only one annual molt is used for the same communication purposes in winter and summer. Thus in such species, if any advantage is conferred by signalling one's status with colour during winter, this should carry over to summer.

The nomadic nature of redpolls makes it difficult to obtain data on their survival rates. The problem of measuring survival rates was approached by Baker and Fox (1978) who conducted experiments with captive juncos in which food was limited. Heavier birds tended to "survive" longer than lighter birds which tended to be low-ranking females. Except for its association with sex, hood colour was not related to "survivorship" in their experiment.

No differences in nesting sites of redpolls were detected (according to the variables that were measured to describe the vegetation in this study). Nests were located randomly with respect to vegetation-type. Those attended by brightly-coloured males, were in habitats similar to those attended by pale males, as were those containing large and small clutches or having relatively high and low hatching success. Rather, redpolls seemed inexacting in their choices of suitable nesting habitat, a point also noted by Hagerup (1891) and Walkinshaw (1948). Moreover, there was no shortage of apparently suitable nesting sites in the areas

studied. These results are similar to those reported by Marler and Mundinger (1975) for Twites (*Carduelis flavirostris*).

Some cardueline finch populations are known to be female-limited during the breeding season (French 1959, Johnson 1965, Samson 1976). If redpolls are also female-limited, implying that females should have a wide choice of males with which to mate, and if brightly coloured males are desirable, then females would preferentially select them. The proportion of colour-types among males known to have been mated was the same as among all males caught, indicating that either males were not preferentially chosen as mates according to colour or that there was no shortage of females.

Some anecdotal evidence found both in the literature and by the author suggests that red-breasted males are equally or possibly less desirable mates than white-breasted males: Hagerup (1891) noted that of the males he observed nesting, none had red breasts; Alsop (1973) reported that two of three male redpolls attending one female brooding eggs on a nest lacked red breasts while the third was highly coloured; and I observed one nest at which two males were present, both of which had intensely red breasts. If brightly-coloured males are at an advantage with respect to mating it is unlikely that they would share nesting duties with another male, especially not with another brightly-coloured one.

Finally, reproductive success as judged by clutch size, hatching success and fledging success of young, varied independently of the breast colouration of fathers. Although reproductive success is the essential test of the prediction that brightly-coloured birds are advantaged during breeding seasons as well as winter, a larger number of nests would have provided a more rigorous test. Nevertheless, I feel justified in rejecting the prediction based on both my observations and evidence in the literature.

B. Experiments

The central prediction of Rohwer's hypothesis, that individual colouration signals social status in a hierarchy, was tested by artificially manipulating plumage colour of some captive birds, and by comparing the brightness of captive birds with their positions in hierarchies.

Artificial Colouration

There are several reports in the literature of experiments in which the colour of a bird in a dominance hierarchy was artificially manipulated; the results differ from study-to-study. For example, Ring Doves (*Streptopelia risoria*), temporarily altered their behaviour towards an artificially-coloured flock-member, which led Bennett (1939) to conclude that individuals in a hierarchy recognized each other. Guhl and Ortman (1953) reached a similar conclusion after observing few changes in a hierarchy of domestic chickens before and after altering their colour or shape.

Bennett (1939) and Guhl and Ortman (1953) suggested that recognition was accomplished primarily through behaviour, supplemented by visual and auditory signals. However, Marler (1955b) observed that female Chaffinches whose breasts had been reddened to resemble that of males, rose in social status. Rohwer and Rohwer (1978) demonstrated that behaviour as well as hood colouration was important to the social organization of Harris' Sparrows. They found that artificially-coloured birds with testosterone implants rose in social status whereas birds that were coloured but not treated with testosterone were persecuted.

In redpolls, enhancement of breast colour did not increase their social status, contrary to Marler's (1955b) observations of Chaffinches. As well, artificially coloured birds did not become the victim of more attacks or perrsecution, as Rohwer (1977) observed in Harris' Sparrows. In conjunction with my field observations of models placed at nests, these results indicate that red breast colouration does not act as a "social releaser" (Tinbergen 1948) as (Lack 1946) and Marler (1955b) reported for English Robins and Chaffinches, respectively. Additionally, breast colour does not appear to signal the status of individuals. I also suggest that individuals in a hierarchy recognize each other by means other than, or in addition to breast colouration based on my observations where artificially colouring one or two of the birds in a hierarchy did not appear to alter the other birds' ability to recognize them. This suggestion

supports Dilger's (1960) comment that redpolls have a well developed ability for individual recognition which he related to their rigid social structure.

Behaviour and Colour

My data demonstrate that an individual's colour is not related to its social status in a hierarchy, regardless of season. It is unlikely that the results obtained were an artifact of the design of the experiments and method of testing the relationship between plumage colouration and social position. The measurements recorded to describe colouration and behaviour and the statistical tests employed to analyze them were more thorough and sensitive than those of previous investigators (Thompson 1960, Dilger 1960, Rohwer 1975, Balph *et al.* 1979, Baker and Fox 1978). Thus, if colour were related to dominance, or another aspect of agonistic behaviour such as aggressiveness, it would have been detected in the data and test results.

My observations of behaviour in the aviaries were similar to those of redpolls in the field. For example, while feeding, redpolls continually engaged in agonistic behaviour, often for no apparent reason. I observed birds of all colours as aggressors and victims. Individuals at a feeder platform were randomly positioned with respect to breast colour; a colour-type did not group together at the centre of the feeding aggregation as Pulliam (1973) would predict if that type were dominant. Nor were those birds that flew down to feed first, took flight when scared, or

initiated feeding of any consistent plumage colour.

Behaviour and Morphology

My data show that agonistic behaviour, measured in various ways, was unrelated to any measure of body size, which strongly confirms similar but weaker tests with passerines by Shoemaker (1939), Tordoff (1954), Thompson (1960), Glase (1973), and Smith (1976). In my analysis body weight, wing length and tarsus length, measurements generally used to estimate body size, were augmented by other external and skeletal measurements so that body size should have been more than adequately reflected. From my observations and those of others in the literature (e.g. Shoemaker 1939, Tordoff 1954, Thompson 1960, Rohwer 1975), there is little evidence for the widely-held belief that in passerines dominant birds are larger in size than subordinate ones.

C. Status Signalling Hypothesis

In light of the observations I have presented, and an examination of the literature, one can justifiably ask if Rohwer's hypothesis holds for any species, and if so, under what conditions. To answer this question I have evaluated the tests of predictions based on his hypothesis that Rohwer performed, and compared his results with experimental evidence from similar studies. As well, I will discuss some theoretical considerations and possible evolutionary mechanisms for the development of status signalling.

Interspecific Tests

Rohwer made three interspecific tests of the prediction that plumage variability is negatively correlated with flock stability. In the first test plumage scores assigned to males of 29 passerine species (based on individual variation and amount of signalling colour), were regressed on scores assigned for their winter flock structure and migratory status. The result of the regression was significant in the predicted (positive) direction. Shields (1977) criticized the plumage variability scores assigned to the species, for their subjectivity and hence lack of repeatability, and for combining diverse types of plumage patterns on one scale. For example colour patterns from species with two discrete age-related plumages and a species exhibiting continuous variability could have received similar scores. Rohwer's (1977) response to this criticism was an explanation of how he dealt with monomorphic, dimorphic and polymorphic species and confirmed the subjective nature of the ranking. As well, the significance of the regression he performed was questionable because it was performed on data that were not suitable for treatment by parametric statistics, for example categorical scores. Nevertheless, the variability scores (from low to high) were positively correlated with winter social structure (from spaced to flocked).

The other two interspecific tests Rohwer presented rely on questionable assumptions and hypotheses not fully tested, that weaken any conclusions that may be drawn from the

tests. Rohwer assumed that diurnal migrants exist in more stable flocks than nocturnal migrants and cited Balcomb (1977) who reported that birds migrating at night mostly do so singly, rather than in flocks. Balcomb's observation does not confirm the assumption that the degree of association between individuals during migration is directly related to their day-to-day flock stability.

Finally, Rohwer attempted to demonstrate that flock stability is related to plumage variability by means of a measure of kinship association. The test was based on the assumption that distress screams given by winter birds have evolved as cries for help through kin selection (Rohwer, Fretwell and Tuckfield 1976). Three assumptions underlie Rohwer's test--that of kin selection (Maynard Smith 1964) or reciprocal altruism (Trivers 1971), distress screams as a measure of kin selection (Rohwer *et al*. 1976), and plumage variability related to kinship (Rohwer 1975). Any outcome of the test between distress screams and plumage variability would only be tenuously related to the final link in the deductive chain as a result of the implicit assumptions. Thus, the final link, that plumage variability is correlated with flock stability, could not be firmly demonstrated by this test.

Intraspecific Tests

In addition to my work, three studies, those of Rohwer (1975), Baker and Fox (1978), and Balph *et al*. (1979), have explicitly tested the status signalling hypothesis, the

latter two with Dark-eyed Juncos. Hood colouration in juncos is related to age and sex. Balph *et al.* (1979) found that darker-hooded juncos won 69 per cent of fights with a lighter-hooded individual. However, darker individuals won only 52 per cent of encounters over lighter-hooded birds of the same sex. Similar results were obtained when birds were grouped according to wing length, another sex-dependent characteristic. Baker and Fox (1978) found a non-significant correlation between hood darkness and dominance rank of captive juncos and calculated that hood colouration contributed 11 per cent to the prediction of "survivorship", dominance rank contributed 30 per cent and body weight 20 per cent. Balph *et al.* (1979), Baker and Fox (1978) and Ketterson (1979b, who indirectly examined hood colouration with respect to agonistic behaviour in wild juncos) agreed that hood colour signals social status in Dark-eyed Juncos only insofar as colour is related to sex and age classes.

My observations on redpolls concur with their comments. Male and adult redpolls tended to be dominant and redder than females and juveniles. However, colour is less well correlated with sex or age class in redpolls than in juncos, hence the low correlation between colour and social status. Balph *et al.* (1979) suggested that the degree of sexual dichromatism exhibited by a species may be related to the extent to which one sex dominates the other: in Evening Grosbeaks (*Hesperiphona vespertina*) which are highly sexually dichromatic, males dominated females in more than

97 per cent of the encounters observed by Balph *et al.*; in juncos, which are less sexually dichromatic than Evening Grosbeaks, males dominated females in 82 per cent of relationships they observed; and in redpolls, the least sexually dichromatic, the number falls to 69 per cent in the pairs I observed.

Rohwer (1975, 1977) did not present data on which to base his conclusion that plumage colouration of wintering Harris' Sparrows is a more accurate predictor of social status than sex or age. His conclusion seems to be at odds with his observation that darker-plumage sparrows won 76 and 70 per cent of encounters, figures comparable to the 69 per cent recorded by Balph *et al.* (1979) for juncos. Thus, the experimental evidence presented to date does not support Rohwer's statement that plumage colouration accurately predicts social status, especially within a sex or age class. The status signalling ability of individual colouration appears to accrue primarily through association with sex and age groups.

Theoretical Considerations

Additional evidence militating against Rohwer's hypothesis comes from theoretical considerations of dominance hierarchies. Chase (1974) examined "statistical" or "tournament" hierarchy formation in which ranks are determined by round-robin fighting, and "correlation" or "signalled" hierarchies in which an individual's social status is correlated with some trait or group of traits.

Through mathematical formulations, tested on data from the literature (mostly from Guhls' (1953, 1968) studies on domestic chickens), he found that the correlation between status and a trait must be very high to allow prediction of rank (for example r=0.88 for a group of 6 individuals). Such high levels of correlation are generally not found in hierarchies that have been studied. Chase admitted that his conclusions may not be applicable to all species forming strong hierarchies. If his results are relevant to Harris' Sparrows, it seems unlikely that hood colouration is correlated highly enough with dominance (at the level Chase proposed as necessary) for the correlation model to operate.

Evolutionary Mechanism

Rohwer (1975) did not propose a mechanism by which individuals would evolve to signal their social status. It is generally accepted that the advantage of dominance hierarchies is reduced levels of aggression (e.g. Allee 1952, Lockie 1956, Smith 1976) and that ability to signal prowess increases the advantage by further lessening aggressive interactions (e.g. Rohwer 1975, Barnard and Burk 1979). Implicit in such arguments is the hypothesis that group selection acts to maintain signals since signalling is advantageous to the group or at least to high ranking birds.

A feasible evolutionary mechanism is especially difficult to construct if fighting within a flock is despotic as Rohwer (1975) reported. Shields (1977) argued that if fighting is truely despotic, pale birds would

provoke attacks from brightly-coloured birds, hence plumage variability within a flock would increase the frequency of of aggression. Contrary to Rohwer's hypothesis, convergence on a single plumage-type or signal would be predicted given Shield's line of reasoning. Also, his argument would contradict Rohwer's prediction that it is advantageous for all birds to assess and advertise rank with signals in order to obviate combat. Rohwer (1977) responded to this criticism with three possibilities, first that kin selection may be operating, second that not all fighting may be despotic and third, that his hypothesis may be invalid.

Given that fights occur between individuals of similar plumage within a flock, Balph *et al*. (1979) proposed that plumage variability would be selected for if there was a cost associated with signalling a status that was not commensurate with fighting ability, such as the loss of energy-expensive fights. This argument may be unnecessary if colour acts as a releaser or conditioned reinforcer (Balph *et al*. 1979) because colour could have evolved for a purpose other than status signalling.

Maynard Smith (1979) briefly examined Rohwer's work in terms of evolutionarily stable strategies, in an attempt to eliminate group in favour of individual selection arguments. He suggested that Harris' Sparrows may be playing either a mixed strategy or a "Hobson's Choice" strategy. If playing a mixed strategy, the sparrows must meet the criterion that the fitness of individuals playing different strategies must

be the same (Maynard Smith 1979). Meeting this criterion runs counter to empirical evidence that subordinate (hence pale) individuals have lower probabilities of survival (e.g. Lockie 1956, Murton 1971). A "Hobson's Choice" strategy depends on some extrinsic factor: an example is, "if large play Hawk, if small play Dove". Harris' Sparrows and juncos may be adopting a "Hobson's Choice" strategy, perhaps based on sex or age rather than size, and colour may cue which strategy will be played. For example, large males that are brightly coloured may play Hawk and behave aggressively whereas small females that are pale may play Dove and behave submissively. The latter strategy may explain the evolution of the association between plumage colour and social status in some species, although this is difficult to test.

Conclusions on Status Signalling Hypothesis

Prior to the presentation of Rohwer's hypothesis several authors (e.g. Collias 1943, Guhl and Ortman 1953) expressed the idea that external characteristics of individuals signalled or at least were correlated with social status. Geist (1966) presented a strong case for correlation between individual appearance and dominance in mountain sheep (*Ovis canadensis*). The status signalling hypothesis as applied to birds is attractive in its ability to account for a broad spectrum of plumage types from monomorphism to continuous inter-individual variability.

Barnard and Burk (1979) raised some interesting points concerning the status signalling hypothesis. First, they

concluded that at least two cues, colour and behaviour, were used by Harris' Sparrows to assess dominance on the basis of Rohwer's (1977) experiments with colour alteration in which individuals only coloured did not rise in rank whereas those coloured and given testosterone implants did (Rohwer and Rohwer 1978). Second, Barnard and Burk drew attention to the false distinction made between "individual recognition" and recognition using one or a few cues in describing how dominance hierarchies are formed. The disagreement between Rohwer (1978) and Shields (1977) on the evolution of colour variability for the purpose of status signalling and individual recognition respectively, therefore reduces to determining whether colour is correlated with social status or not.

The lack of an easily testable hypothesis that could account for the evolution of colour as a signal of dominance in a hierarchy (the hypotheses listed above have yet to be tested) is a weakness of Rohwer's hypothesis: it remains to be shown how a signal detrimental to its bearer could evolve. This weakness however, does not invalidate Rohwer's argument.

Based on my observations and those in the literature, I conclude that plumage colour is very weakly related to social status in winter hierarchies. As Ketterson (1979a) pointed out, despite the low predictive power of an individual's colour within a sex and age class, Rohwer's hypothesis could explain why these, or any other classes are

distinguishable by plumage colour in the non-breeding season. Alternatively, colour may have evolved for other purposes and may only be a releaser or conditional reinforcer (Balph *et al.* 1979), although I have presented evidence suggesting that breast colour in redpolls does not act as a releaser. Either way, I feel Rohwer (1975, 1977, 1978) was unjustified in concluding that colour is an "excellent" predictor of status in Harris' Sparrows or any other species, and that colour has evolved solely to signal status in species that are variably-coloured in winter.

D. How Are Hierarchies Formed in Redpolls?

Redpolls do form strong hierarchies in captive situations, and wild birds exhibit dominance behaviour and may exist in hierarchies. The question remains open as to how rank is determined in redpoll hierarchies.

Barnard and Burk (1979) suggested that hierarchies may be formed in three ways: (1) through round-robin competitions, (2) by the relative "confidence" of individual based on previous wins and losses, and (3) by assessment of some cue or cues related to an individual's competitive ability. Redpolls do not appear to employ either the first or second method in determining rank. This belief is based on low numbers of encounters involving any fighting that I observed (particularly in winter), even when birds were introduced to the aviary: subordinates deferred to dominants without visible combat. There is no evidence that an

individual uses one, or more than one, morphological or plumage colour characteristics by which to assess the fighting ability of others. Rather, I suggest that redpolls form assessment hierarchies, with the behaviour of individuals taken as cues of fighting ability. Guhl and Ortman (1953) offerred a similar suggestion concerning rank establishment in domestic chickens. A bird's behaviour is not always commensurate with its fighting ability as evidenced by individuals occasionally loosing encounters that they initiated (success scores less than one). Actual fighting ability is the final arbiter of rank if an ambiguity arises or some individuals are of similar status. My data do not illustrate this *per se*, but indirectly they show that rank was highly correlated with behaviour variables, all of which are interdependent as they were derived from the same set of interactions. Stronger evidence on which to base this suggestion was the infrequency of overt aggression that I observed, and the low number of rank changes within hierarchies. Barnard and Burk (1979) predicted that rank changes should occur in "confidence" but not assessment hierarchies. In my study, if a subordinate did not defer to a dominant individual, aggressive encounters escalated until one bird retreated.

E. Source of Variability in Redpoll Colouration

Colouration of redpolls and other cardueline finches continues to be an enigma. Is redpoll colouration related to the ecology or social system of the species or is their red colouration a neutral characteristic uninfluenced by selection pressures? I agree with Johnson and Brush (1972) who, in a study of the colouration of bush-tanagers (*Chlorospingus pileatus* and *C. zeledoni*), rejected the idea that colouration was a neutral characteristic:

> We do not accept the thesis that the examples of visible phenotypic difference which characterize polymorphism in birds are selectively neutral, even if they are maintained in part as byproducts of a "genetic physiological mechanism that is favored by selection (Mayr 1963:157)". For one thing, the high degree of reliance of many species of birds on visual communication in the organization of social systems suggests that colors and patterns of plumage relate importantly to success in pairing and, therefore, to reproductive fitness. This implies that there is a modality of pattern and color of plumage, from which significant departures are costly in terms of social, and hence reproductive, success.

In order to test if a species' colouration is adaptive it is necessary to demonstrate that individuals are less successful after their colour has been altered, as has been

done with Red-winged Blackbirds (*Agelaius phoeniceus*; Peek 1972, Smith 1972), Yellowthroats (*Geothlypis trichas*; Lewis 1972), and Village Weaverbirds (*Ploceus cucullatus*; Collias *et al.* 1979) to mention a few. I contend that a red rather than white breast renders a redpoll more obvious to avian predators by decreasing the bird's crypticity. Because the species is probably vulnerable and palatable, as are its congeners Twites and Linnets (*Carduelis flavirostris* and *C. cannabina*; Cott 1946), it is a reasonable conjecture that an individual must benefit in some way from the bright colouration.

In the introduction I listed several hypotheses that have been proposed to explain avian colouration, of which only the status signalling and individual recognition hypotheses could account for inter-individual variability. Individual recognition is here considered to be unrelated to dominance behaviour. In the foregoing I have demonstrated that Rohwer's status signalling hypothesis does not hold for redpolls. Based on my observations, I submit that redpolls exhibit inter-individual colour variability for the purpose of individual recognition.

Individual Recognition

It has been amply documented that many birds, usually mates or other family members, can easily identify each other. Individual recognition by means of voice has been documented experimentally in, for example, Ovenbirds (*Seiurus aurocapillus*; Weeden and Falls 1959),

White-throated Sparrows (*Zonotrichia albicollis*; Brooks and Falls 1975), Zebra Finches (*Poephila guttata*; Miller 1975), American Goldfinches and European and Pine Siskins (*Carduelis tristis*, *C. spinus*, and *C. pinus*; Mundinger 1970). Accounts of recognition by visual means are mostly anecdotal. Examples include Marsh-tits (*Parus palustris*; Morley 1942), European Robins (Lack 1939), Pintails (*Anas acuta*; Hochbaum 1944) and Jackdaws (*Corvus mondedula*; Lorenz 1931), all of which were reported to recognize mates or flock-mates at distances up to 60 to 300 metres. In one of the few experiments conducted on visual recognition, Trillmich (1976) demonstrated that Budgerigars (*Melopsittacus undulatus*) trained to respond to projected images of conspecifics, could distinguish between individuals when presented with two choices.

Recognition of individuals has been hypothesized to be important in species in which social relationships are protracted, parental care continues after young have fledged, in colonial situations, and when a species is not philopatric and individuals show fidelity to other individuals rather than to a place (Thorpe 1968, Beer 1970, Samson 1978). Vocalizations among individuals may be more variable and hence aid in individual recognition when voice is not constrained by use for territorial advertisement and defense (Marler 1961, Thorpe and North 1966, Thorpe 1958, 1968). Vocalizations would be particularly important in environments where vision is obscured such as in dense

forests or coastal water (Thorpe and North 1966, Thorpe 1968). Optical signals, which provide a wider range of cues for recognition (Thorpe 1968), would be favoured in open habitats (Beer 1970) and in species freed from intense predation pressure (Marler 1957).

I offer three reasons for the use of colour for individual recognition by redpolls. The first two points, inter-individual variability and the position of the red colouration, were discussed earlier in connection with the use of colour as an intraspecific communciation signal. The third point concerns the general biology of the species.

Four aspects of redpoll biology would favour well developed abilities to recognize other individuals. First, redpolls flock year-round, even during the breeding season, and mating takes place while birds are in large winter flocks. Such gregariousness is analagous to colonial breeding systems in which fast and accurate mate recognition is at a premium (Thorpe 1968, Beer 1970). Second, redpolls are not philopatric, and they show fidelity to mates while breeding, rather than territories. In species that are site tenacious and territorial, mate recognition is secondary to recognition of territory (Beer 1970). Third, redpolls develop relatively strong relationships during the breeding season: their monogamous pair bonds persist for at least one month and young may be fed for up to two weeks after they leave the nest. For example, Newton (1972) reported that young European Goldfinches are fed for at least 10 days

after leaving the nest, and Linnets and Twites at least 15 days. It is of course important to recognize mates and young when a family member cares for another (Thorpe 1968). For example, female redpolls on the nest are fed by their mates during incubation and post-hatching periods. Finally, redpolls frequent open habitats, where colour signals can be easily seen (Beer 1970, Hailman 1977), such as tundra, open boreal forest (with discontinuous canopy cover) and prairies.

Variations in the colouration of redpolls are consistent with the individual recognition hypothesis. Perhaps most important is that red colouration, and consequently colour variability, within a population reaches a maximum during the breeding season when recognition of mates and young is required. Hoary-types, which attain only pink breasts, inhabit more open habitat in which optical signals are more easily seen than in forests inhabited by the redder common-type. Hoary birds are also whiter than commons which supports Hailman's (1977) hypothesis that species living in environments with low levels of irradiance (such as high latitudes) should use light colours, particularly white, as optical signals. Differences in the range of breast colours attained by sex and age classes may be explained by their relative vulnerability. Crypsis is probably paramount to inexperienced juveniles and females who remain on the nest during incubation and early fledging periods (which are relatively vulnerable; Baker and Parker

1979), and so outweighs any advantages accruing from possession of a red breast. Females do acquire pink breasts, but how common this is, or whether it is age-related is unknown.

Two studies of related species bear directly on the hypothesis of individual recognition as applied to redpolls. Samson (1978) noted wide variability in the vocal repertoire of individual Cassin's Finches, and suggested that their songs, which are not used for territorial defense in this nomadic species, may aid in maintaining flock composition. Variable vocalizations also allow for individual recognition of mates, which could facilitate pair-bonding while the birds associate in winter flocks, and recognition of mates from year-to-year.

In contrast to the large vocal repertoire of Cassin's Finches, Marler and Mundinger (1975) found the vocal repertoire of Twites to be unusually small for passerines, even for a cardueline. However, this species exhibits variability in the amount of red colouration on the rump. Twites are similar to other carduelines in their tendency to flock year-round and males defend a territory centred on their mate rather than on a site, and so accompany females whenever they leave the nest. Marler and Mundinger proposed that Twites use visual signals in the open habitat in which they nest, thereby reducing dependence on vocalizations, although it appears mates recognize each other's voices (Mundinger 1979). The signalling ability of the rump patch

is enhanced by "sentinel" behaviour and other postures assumed by males that expose the rump.

General Applicability of the Hypothesis

Further examination of the individual recognition hypothesis is necessary before its general applicability and importance to redpolls and other avian species is known. For those species in which individual recognition is important (those that flock year-round, colonial nesters, nomads, and so on), I predict a high degree of variability in either voice or plumage, whichever modality is used most for signalling. Voice should be used for recognition in species under heavy predation pressure from predators with colour vision or species that frequent dense habitats such as forests. Alternatively, species using plumage as a signal would be expected to be lightly preyed upon or to live in open habitats. Neither voice nor plumage need be used exclusively as signals; combinations best suited to the situation of particular species would be expected.

The individual recognition hypothesis can be well illustrated in the redpoll genus *Carduelis*. All species of this genus exhibit social systems very similar to that of the redpoll--individuals are social, they flock year-round and nest semi-colonially. One group of species in this genus, those formerly of the genus *Spinus* (Greenfinch, Siskin and European and American Goldfinches) are all yellow or greenish and inhabit closed habitats such as thickets and forests (Newton 1972). I suggest that they achieve

individual recognition primarily through voice. Mundinger (1970) demonstrated that goldfinches and siskins recognized their mates' call which was very similar to their own. The similarity of calls between mates and among all flock members resulted from the well developed learning ability of these birds. New flight calls could be learned by imitation at any age within both pairs and flocks. The other group of species, formerly *Acanthis*, or redpoll-like species (Linnet, Twite and Redpolls), all exhibit varying amounts of red on their rump, throat or cap depending on the species and sex. Newton (1972) described these birds as scrub-dwelling or inhabiting open country. I propose that individual recognition is accomplished primarily through plumage variability although there is no doubt that voice remains important (Mundinger 1979). Marler and Mundinger's (1975) study of Twites is instructive here.

Chaffinches and Bramblings (*Fringilla coelebs* and *F. montifringilla*) provide a contrast to the *Carduelis* species. The former show strong sexual dichromatism and have well developed songs; both plumages and songs are used for territorial defense (which Lack (1968) and Newton (1972) suggested is associated with their insectivorous diet). In these highly territorial species, I suggest that recognition is primarily site related. Secondarily, recognition of individuals, such as neighbouring territory-holders, is probably through voice as in territorial White-throated Sparrows (Brooks and Falls 1975). Sexual recognition may be

facilitated by their characteristic plumages (Hamilton 1961, Rowland 1979).

Finally, at the opposite end of the plumage variability continuum from redpoll-like carduelines, are species of low colour variability such as Bullfinches and parids (chickadees and titmice). Bullfinches are sexually dichromatic carduelines with a very simple plumage pattern. Nicolai (1956) reported that they mate for life. Parids are site tenacious and territorial; individuals may remain associated over several years in the same location (Wallace 1941). I suspect that recognition is in part site related and is also achieved through subtle plumage and vocal differences, made possible by the length of time over which individuals remain associated.

Plumage colouration of numerous other species can be explained by interplay of the factors listed above. By proposing the individual recognition hypothesis I am by no means assuming that this or any other single hypothesis could acocunt for the many and diverse facets of avian colouration patterns.

The predictions I have enumerated from the individual recognition hypothesis could be tested in three ways. The first test uses the comparative method (Hailman 1977:13) whereby species found in different environmental conditions, and differing in behaviour are examined to determine if they meet the predictions of the hypothesis. Although I have compared several species differing in habitats in which they

are found, behaviour and colour variability, a more thorough test should include more species of as diverse a range of characteristics as possible. For example, Pine Grosbeaks (*Pinicola enucleator*) and Red and White-winged Crossbills (*Loxia curvirostra* and *L. leucoptera*) exhibit extensive plumage variability that is in stark contrast to the very uniformly coloured waxwings (Bombycillidae) and flycatchers (Tyrannidae). However, comparing the various characteristics of species provides only circumstantial evidence and thus is not a powerful test of the predictions.

The second test, more potent than the first, directly examines the individual recognition hypothesis by means of individuals trained to discriminate between conspecifics on the basis of visual appearance alone. Trillmich's (1976) extensive and elegant experiments with trained Budgerigars provide the best example of such tests. Trillmich trained birds to choose (by using positive reinforement of correct choices), between individuals, projected images of individuals, vocalizations, and images and vocalizations together. Subjecting trained redpolls to such an experimental regime would allow the experimenter to distinguish cues used by the birds in making their choice. For example, Trillmich determined that the features of the head were used predominantly for discrimination by the budgerigars tested, by concealing various parts of the 'object' birds (those presented to the bird making the choice). He also found that the birds relied on visual

appearance more than vocalizations by simultaneously subjecting trained birds to images and vocalizations and changing the vocalizations presented with the image. Experiments such as this would have to accommodate the more nervous nature of redpolls than budgerigars, and must be designed to enable distinction between plumage colour and other individual characteristics such as shape.

The third test of the hypothesis involves wild redpolls. This test could be accomplished by subtly altering the colour of one member of a mated pair and observing the reaction of the other bird to its altered mate. Mated pairs are necessary for use in the experiment because other individuals are too unpredictable in their associations to allow sufficient observation of interactions before and after colouration. A test of the individual recognition hypothesis would require more refined techniques of colour alteration than those performed in similar experiments that have examined cues used for sexual recognition (e.g. Noble and Vogt 1935, Lewis 1972).

VII. SUMMARY and CONCLUSIONS

In the study reported here, I have tested Rohwer's (1975) status signalling hypothesis that states that plumage variability, which is related to the social structure of avian species in winter, has evolved to signal the approximate status of individuals in dominance hierarchies. I also tested an extension of Rohwer's hypothesis, that brightly coloured individuals (those predicted to be dominant) should enjoy higher reproductive fitness than pale (subordinate) individuals. Redpolls were chosen as a species with which to test the hypothesis because of their plumage variability and tendency to associate in flocks.

Contrary to the prediction, I found that breast colouration of male and female redpolls was not correlated with nesting success, territory quality or frequency of mating during the breeding season. In order to test Rohwer's major prediction that more brightly coloured individuals (those with redder breasts), should dominate pale or white-breasted ones, I conducted experiments with captive birds in winter and summer. Individuals that were artificially reddened in these experiments, did not increase in dominance status as Marler (1955b) reported for similar experiments with Chaffinches, or suffer persecution after treatment as Rohwer (1977) observed with artificially blackened Harris' Sparrows. Contrary to the prediction, agonistic behaviour (described by the variables dominance, success, victimization and aggressiveness), was not

correlated with breast colour of test birds (represented by dominant hue, purity or brightness) regardless of season, morph (common or hoary), or level of aggression. Neither was the size of the birds (described by seven external body measurements and 19 skeletal measurements), correlated with their agonistic behaviour. These results support numerous weaker tests that provide evidence contradicting the generally held belief that larger birds dominate smaller ones.

Therefore, based on my observations and those reported by others who have tested the status signalling hypothesis, I conclude that colour signals dominance insofar as both colour and dominance are sex- and age-related characteristics in many species. I agree with the suggestion made by Balph *et al.* (1979) that colour, instead of cuing dominance, acts as either a releaser or a conditional reinforcer. However, there is no evidence that breast colour acts as a releaser in redpolls.

As an alternative to Rohwer's hypothesis, I suggest that relative dominance in redpoll hierarchies is determined by the assessment of the behaviour of individuals as an indication of their fighting prowess. Fighting ability is the final arbiter where disputes occur.

Returning to the central question of avian colouration, and more specifically the colour variability exhibited by redpolls, I submit that variability facilitates individual recognition, which is important to individuals because of

their social system; individuals flock year-round (including during the breeding season); pair formation occurs while they are in large winter flocks; the species is nomadic, showing neither winter or summer philopatry; and they nest semi-colonially with no site-related territorial defense. The individual recognition hypothesis can account for variability in visual or vocal signals, or the lack of them, in other carduelines and possibly passerines in general.

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APPENDIX 1

List of captive birds that were in experiments. Collection number preceeded by MLD indicates that the individual was taken as a specimen. Number preceeded by L indicates that the bird escaped. Sex of individuals is specified by M for male, F for female and ? for unknown. Breast colour scores were subjectively assigned to birds on a scale of 0 for no red, to 5 for an extensive and bright red breast. BN and tarsus refer to bill length and tarsometatarsus lengths respectively. An asterisk beside a collection number indicates that the individual was artificially coloured red, a cross indicates an individual was artificially coloured green. The breast colour scores of artificially coloured birds refer to their pre-colouration appearance.

Experiment Dates	Collection Number	Rank	Sex	Breast Colour	BN	Tarsus
Winter						
16/2 - 2/3/78	MLD 100	5	F	1	7.4	16.6
	MLD 89	4	M	0	6.6	17.5
	MLD 99	3	M	3	7.3	16.2
	MLD 97	2	M	4	7.7	16.0
	MLD 98	2	M	4	7.6	16.8
	MLD 90*	0	F	0	6.8	16.0
9/3 -17/3/78	MLD 110	4	F	0	6.2	15.0
	MLD 108	3	M	0	6.8	15.1
	L 122	3	?	2	6.7	15.8
	MLD 109*	2	F	0	7.0	15.5
	MLD 107	2	F	0	7.6	14.5
	L 123	1	?	2	7.0	13.9
19/3 -27/3/78	MLD 119	4	M	1	7.2	15.7
	MLD 120	3	M	2	6.7	14.9
	MLD 118	3	M	3	8.0	15.0
	MLD 117	3	M	0	7.0	15.2
	MLD 116*	1	M	1	7.1	16.0
	MLD 115	1	M	3	6.8	15.8
28/3 - 7/4/78	MLD 121	5	M	1	6.7	14.7
	MLD 120	4	M	2	6.7	14.9
	MLD 124	3	F	0	7.4	15.4
	MLD 123*	2	M	1	7.6	15.6
	MLD 122	1	F	0	6.4	14.5
	MLD 144	0	M	2	7.8	15.0

Experiment Dates	Collection Number	Rank	Sex	Breast Colour	BN	Tarsus
9/4 -19/4/78	L 128	5	M	3	7.3	15.8
	MLD 126	3	M	3	7.4	15.2
	MLD 144	3	M	2	7.8	15.0
	L 125+	2	F	0	7.4	15.3
	L 127*	1	M	1	7.1	14.9
	L 124	0	F	0	6.6	14.7
10/12-15/12/78	MLD 264+	5	M	1	7.2	14.5
	MLD 262*	4	M	0	6.8	15.1
	MLD 259	3	M	1	7.3	15.4
	MLD 263	2	M	0	7.1	14.9
	MLD 265	1	M	2	6.2	14.0
	MLD 261	0	M	2	7.5	15.6
27/1 - 4/2/79	MLD 270	5	M	1	7.1	15.7
	MLD 271	4	F	1	7.2	14.8
	MLD 267	3	M	2	7.6	14.1
	MLD 268	1	M	2	7.5	15.2
	MLD 269*	1	M	3	8.2	14.1
	MLD 266+	1	F	0	7.8	16.1
Summer						
11/7 -26/7/78	MLD 209*	5	M	0	7.8	16.0
	L 92	4	M	4	7.8	14.5
	MLD 210	3	F	0	6.7	17.5
	L 90	2	M	2	6.9	16.2
	MLD 211+	1	M	0	6.2	16.8
	L 91	0	F	0	6.5	16.2

Experiment Dates	Collection Number	Rank	Sex	Breast Colour	BN	Tarsus
26/7 - 1/8/78	L 92	5	M	4	7.8	14.5
	MLD 186	4	M	3	7.4	15.6
	MLD 207*	3	M	0	7.6	17.2
	MLD 208	2	M	2	7.1	16.3
	MLD 210	1	F	0	6.7	17.5
	L 91	0	F	0	6.5	16.2
4/8 - 9/8/78	MLD 226	4	M	2	7.0	14.9
	MLD 227	4	F	0	5.7	15.2
	MLD 260	3	F	0	6.5	13.7
	MLD 215+	3	M	2	7.0	14.9
	MLD 213*	1	M	0	6.2	15.7
	L 103	0	F	0	7.2	15.1
10/8 -22/8/78	MLD 226+	5	M	2	7.0	14.9
	MLD 224	4	M	2	7.1	15.5
	MLD 225	3	F	0	6.5	15.8
	MLD 227	2	F	0	5.7	15.2
	MLD 229	1	M	4	7.2	15.7
	MLD 228*	0	M	1	7.5	15.7

APPENDIX 2

Description of skeletal measurements taken on redpoll specimens (from Troy, pers. comm.).

Measurement	Description
1. Premaxilla length	length from posterior end of external nares to tip of premaxilla
2. Premaxilla width	width just anterior to lateral projections near base of upper bill
3. Gonys	medial length of dentary symphysis
4. Mandible width	maximum width of lower bill
5. Coracoid length	maximum length
6. Furcula length	maximum distance from furcular process to acromion process
7. Scapula width	width of anterior end from the glenoid to the process where the scapula articulates with the coracoid
8. Humerus length	maximum length
9. Ulna length	maximum length
10. Radius length	maximum length
11. Femur width	maximum transverse distance from head to flattened, lateral surface of proximal end of femur
12. Tibiotarsus length	maximum length
13. Tibiotarsus width	maximum width of distal end of tibiotarsus where it articulates with the tarsometatarsus
14. Tarsometatarsus length	length from subterminal projection at proximal end of tarsometatarsus to the trochlea for phalanx III
15. Hallux length	maximum length of phalanx I

Measurement	Description
16. Sternum length	maximum distance from anterior end of manubrial spine to centre of posterior edge of sternum
17. Keel length	medial distance from posterior edge of sternum to anterior (ventral) edge of keel
18. Keel depth	maximum depth of keel including lip on dorsal surface of sternum
19. Synsacrum width	maximum width of synsacrum dorsal to the foramina where the femurs articulate